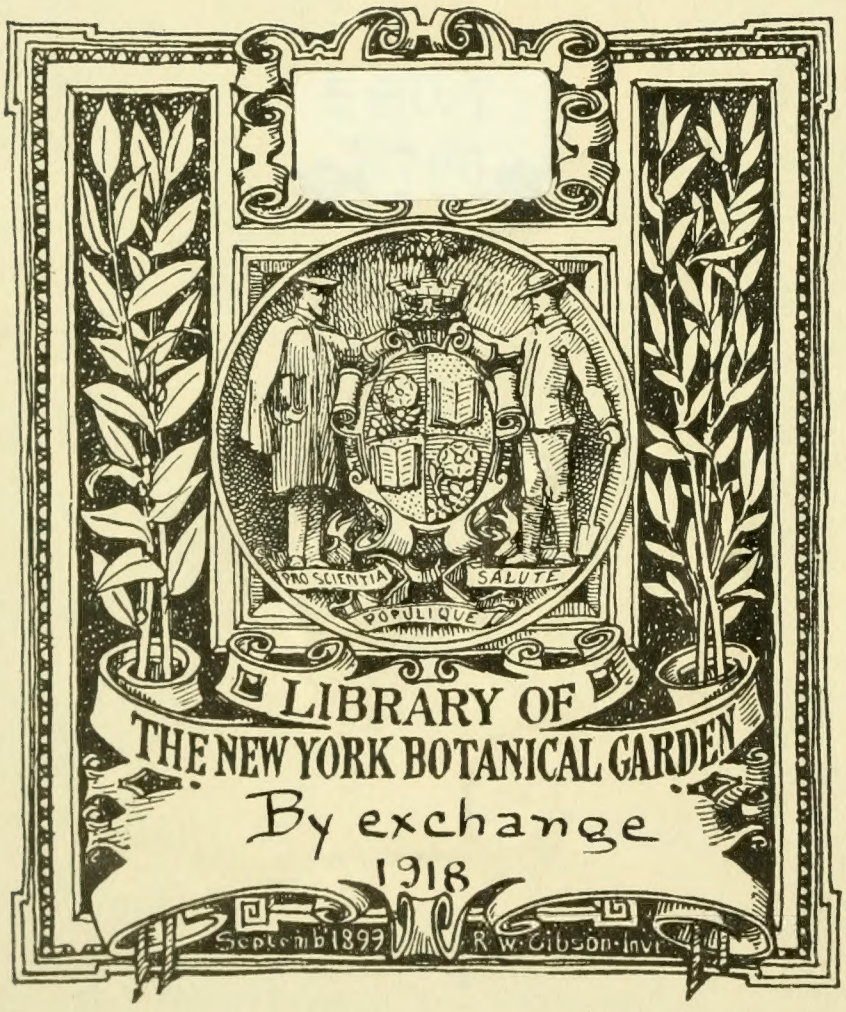

PRO SCIENTIA
SALUTE
POPULIQUE
LIBRARY OF
THE NEW YORK BOTANICAL GARDEN
By exchange
1918
Septemb 1899
R W Gibson Invt

Brooklyn Botanic Garden

# BROOKLYN BOTANIC GARDEN

# MEMOIRS

## VOLUME I

## DEDICATION PAPERS

ISSUED JULY 6, 1918
BROOKLYN, N. Y., U. S. A.

BROOKLYN BOTANIC GARDEN

# MEMOIRS

## VOLUME I

## DEDICATION PAPERS

SCIENTIFIC PAPERS PRESENTED AT THE DEDICATION OF THE LABORATORY BUILDING AND PLANT HOUSES

APRIL 19-21, 1917

LIBRARY
NEW YORK
BOTANICAL
GARDEN.

ISSUED JULY 6, 1918

BROOKLYN, N. Y., U. S. A.

XM
.E537
v.1

PRESS OF
THE NEW ERA PRINTING COMPANY
LANCASTER, PA.

# PREFACE

The papers contained in this volume were presented on April 20–21, 1917, either in person or by title, at the Scientific Program, which formed part of the Dedication Exercises on the occasion of the completion of the Laboratory Building and Plant Houses of the Brooklyn Botanic Garden.

ORLAND E. WHITE,
EDGAR W. OLIVE,
ALFRED GUNDERSEN,
*Publication Committee*

# CONTENTS


PAGE

ATKINSON, GEO. F. The genus *Endogone* . . . . . 1
BLAKESLEE, A. F., and B. T. AVERY, JR. A vegetative reversion in *Portulaca* . . . . . 18
BRITTON, N. L. The flora of the American Virgin Islands . . . . . 19
BURNS, GEORGE P. Weather conditions and plant development . 119
COOK, MEL T. Modern applications of botany . . . . . 123
DODGE, B. O. Studies in the genus *Gymnosporangium*—I. Notes on the distribution of the mycelium, buffer cells, and the germination of the aecidiospore . . . . . 128
EAST, E. M. Intercrosses between self-sterile plants . . . . . 141
HARPER, R. A. Binary fission and surface tension in the development of the colony in *Volvox* . . . . . 154
HARRIS, J. ARTHUR. Further studies on the interrelationship of morphological and physiological characters in seedlings of *Phaseolus* . . . . . 167
HARSHBERGER, JOHN W. American heaths and pine heaths . . . . 175
HOLLICK, ARTHUR. Some botanical problems that paleobotany has helped to solve . . . . . 187
HOWE, MARSHALL A. Further notes on the structural dimorphism of sexual and tetrasporic plants in the genus *Galaxaura* . . 191
JACKSON, H. S. The *Uredinales* of Oregon . . . . . 198
JEFFREY, EDWARD C. Evolution by hybridization . . . . . 298
KUNKEL, L. O. A method of obtaining abundant sporulation in cultures of *Macrosporium solani* E. & M. . . . . 306
MACFARLANE, JOHN MUIRHEAD. Synchronism in plant structures 313
METCALF, HAVEN. The problem of the imported plant disease as illustrated by the white pine blister rust . . . . . 327
MURRILL, WILLIAM A. The rosy-spored *Agarics* of North America 334
OLIVE, EDGAR W. The cytological structure of *Botryorhiza Hippocrateae* . . . . . 337
OSTERHOUT, W. J. V. The nucleus as a center of oxidation . . . . 342
REED, GEORGE M. Physiological specialization of parasitic fungi . . . . . 348
ROWLEE, W. W. Relation of marl ponds and peat bogs . . . . . 410
SHEAR, C. L. Pathological problems in the distribution of perishable plant products . . . . . 415
STEWART, F. C. Tubers within tubers of *Solanum tuberosum* . . . 423

SHULL, GEORGE HARRISON. The duplication of a leaf-lobe factor in the shepherd's-purse . . . . . 427
SINNOTT, EDMUND W. Isolation and specific change . . . . . 444
SMITH, ERWIN F. The relations of crown-gall to other overgrowths in plants . . . . . 448
STONE, GEORGE E. Contact stimulation . . . . . 454
STOUT, A. B. Duplication and cohesion in the main axis in *Cichorium Intybus* . . . . . 480
TAYLOR, NORMAN. A quantitative study of Raunkiaer's growth-forms as illustrated by the 400 commonest species of Long Island, N. Y. . . . . 486
TRELEASE, WILLIAM. The ancient oaks of America . . . . . 492
TRUE, RODNEY H., and HARVEY, R. B. The absorption of calcium salts by squash seedlings . . . . . 502
WHITE, ORLAND E. Inheritance studies on castor beans . . . . . 513

# THE GENUS ENDOGONE

GEO. F. ATKINSON

*Cornell University*

The genus *Endogone* was founded by Link in 1809, and for more than a century its life history and taxonomic relationship have remained very obscure. Notwithstanding this obscurity in relationship and development, the structure of the mature plants is so simple and characteristic, that comparatively few species have been accredited to the genus which do not belong here. The fruit bodies are pulvinate, rounded to reniform or irregular. In size they vary from 2–4 mm. up to 2–3 cm. In life relation they are saprophytes. In habitat they are hypogeous, epigeous or epixylous; and occur under or on the ground, among or underneath fallen leaves, among the rhizoids of mosses or roots of ferns, on dead wood, on sphagnum or other mosses. In color they are whitish to yellow, brown or blackish. Approximately seventeen species are known. The genus is cosmopolitan in distribution. Species are known from Europe (including European Russia), Ceylon, Tasmania, North America, Central America, South America and the Fiji Islands.

*General structure of the fruit body.*—There is a peridium of slender, interwoven hyphae formed by the terminal branchlets of the hyphae which spring from the basal region, branch profusely and radiate to the periphery. The interior constitutes the "gleba," the base or central portion of the "gleba" is sometimes hollow or of less density than the broad peripheral zone. The "gleba" is usually packed with numerous, large thick walled "resting spores," oval, elliptical, or spherical in form, and yellowish, grayish or dark brown in color according to the species. These "resting spores" are 40–100 $\mu$ in diameter, are packed among the hyphae, and terminate certain branches. They have been termed spores, sporangia, ampullae, or asci, the latter term apparently having the preference, since it is employed by a majority of writers. Several large elliptical spores in an "ascus" have been described in one species (*Endogone pisiformis*), a single large spore[1] in an ascus in another species (*E. reniformis*), and numerous minute spores in an ascus in several species. It is

[1] The spores in this species are probably the ordinary "resting spores," the "asci" of authors, for Bresadola (1896, p. 297) says that neither the asci nor their mode of dehiscence was seen.

doubtful, however, if true sporulation has ever been observed. In dead resting spores the contents often segregate into a number of large, rounded or elliptical bodies. In *E. reniformis* the single spore in an "ascus" is probably the "resting spore" itself, while in the species described as having numerous minute sporidia in an ascus (often with an interrogation), the supposed sporidia are probably the numerous fat bodies conspicuous in some species.

## Origin and Development of the "Resting Spores" in Endogone lactiflua Berk.

*Character of the mycelium.*—The only important contribution to development in the genus *Endogone*, thus far, was made by Bucholtz in 1912, in his study of *Endogone lactiflua*. This species is subterranean and occurs in various parts of Europe. The fruit bodies range in size from 4 mm. to 2 cm. The material studied by Bucholtz was found in a plantation of *Abies sibirica* in Livland, Russia. The mycelium is coenocytic, profusely branched, the hyphae following a very sinuous course, but the general direction is radial and toward the periphery. It is non-septate, true cross walls being formed only in connection with the reproductive organs, though false cross walls are occasionally found in the vegetative hyphae. The hyphae vary greatly in diameter, in general becoming more slender toward the periphery of the fruit body, but irregularities in the form of swellings occur. Terminal branches on the interior are often clavate. Sack-like enlargements occur from which numerous branches often diverge. The walls of the hyphae are thick. The nuclei are minute, very numerous, and lie in a parietal layer of cytoplasm.

*The progametes and conjugation.*—The progametes are clavate and of unequal size. They lie nearly parallel and their walls fuse at the lateral point of contact a short distance from the free ends. The nuclei in the progametes, lying near the periphery become larger, more distinct, and undergo one division. The nuclei now retreat from the terminal portion of each progamete and all except one are excluded from each gametangium by a cross wall. A few sterile nuclei sometimes remain in the gametangium but soon degenerate. The origin of the selected gamete nucleus in each gametange is not known, but it is probably derived from one of the peripheral nuclei in the progamete, or one of the daughter nuclei after mitosis. These gamete nuclei are much larger than the progamete nuclei, thus maintaining the nucleo-cytoplasmic relation. Each one occupies the center of its gametange. The walls at the point of contact are now resorbed. The nucleus from the smaller gametange (antherid) migrates into the larger one (oogone).

*Formation of the "resting spore" and simple zygocarp.*—The "resting spore" in *Endogone lactiflua* is not formed in the immediate zygote resulting from the fusion of the two gametangia nor in the oogone, but in an outgrowth from the latter. During and immediately after fusion of the two gametangia their walls become thickened and firm, so that they can not yield to the pressure from the young growing zygote. As a result there arises a sack-like outgrowth from the end of the oogone into which the cytoplasm from the two gametangia flows accompanied by the two gamete nuclei, the antheridial nucleus following the oogonial nucleus. The sac-like outgrowth enlarges into an oval or broadly elliptical resting zygote. A thick, stratified, hyaline, cartilaginous wall is formed next to the primary zygote membrane, which entirely encloses the cytoplasm and other contents, thus separating them from the empty oogone. The two gamete nuclei lie side by side in the center of the zygote but do not fuse until after the resting period, except in a small variety from Germany in which the gamete nuclei fuse at once according to Bucholtz. During the growth and ripening of the zygote it becomes enveloped by slender branches which coil in a more or less spiral manner around it forming a thick cover of small cells, 2–3 cell layers deep, the walls of these cells become greatly thickened and fuse next the zygote, grading out to the thin walls of the surface. Each resting spore, or zygote, with its individual cellular envelope forms a simple fruit or simple zygocarp (zygosporocarp, as Bucholtz terms it). The fruit body of *Endogone lactiflua* is filled with these simple zygocarps intermingled with the mycelium, and is therefore a compound zygocarp. Germination of the "resting spores" has not been observed. *Endogone lactiflua* is the only species of the genus in which such simple zygocarps are known, *i. e.*, a fruit body with a single zygote enclosed in its individual envelope.

## Endogone sphagnophila

In July, 1916, a day or two before the close of a fungus foray organized by Mr. F. C. Stewart at his camp on Seventh Lake, in the Adirondacks, Mr. W. H. Sawyer, Jr., a member of the party, brought in some sphagnum on which were rounded, pulvinate, orange-yellow bodies resembling the plasmodiocarps of certain slime molds. A preliminary examination of the internal structure revealed the fact that it was not a slime mold, but apparently a phycomycete with large resting spores having a thick, hyaline, stratified, cartilaginous wall, and orange-yellow content. A pair of stalks, or suspensors, attached to one end of the resting spores in different stages of development, indicated that they had their origin in an interesting type of conjugation. In the afternoon of the same day (July 31, 1916) Mr. Sawyer

and I crossed the lake and visited the same spot in order to collect more material. The dry weather during the latter part of July had lowered the water in the ravines so that this particular sphagnum moor was water-free although the ground was very soft and wet. The fruit bodies of the fungus were not very abundant, but here and there a single one was found on a sphagnum plant, rarely two or more. In nearly all cases the fruit body was attached on the upper side of the central part of the terminal rosette, or one of its radiating branches. Rarely was a fruit body found attached to one of the lower branches. Altogether some 30 or 40 fruit bodies were collected. A number were fixed in Flemming's solution, some in Biondi's solution and some in chrom-acetic solution. Other material was carried to Ithaca on the living sphagnum, where a few more fruit bodies were fixed. Some were kept during the winter in moist situations out of doors, and others in doors in a dried state. Finally, during the winter of 1916–17, it was revealed to me in a semi-vision, that this fungus was a member of the interesting genus *Endogone*.

*Structure of the fruit bodies, or complex zygocarps.*—The plants are 2–4 mm. in diameter, pulvinate, concave below and convex above, so that a section through the center parallel with the morphological axis is reniform. The larger plants are slightly convoluted or mildly lobed, the upper portion showing two to three broad, low convolutions. As the resting spores mature the plants are orange-yellow in color, but the pigment resides entirely in the spore content, the mycelium and spore walls being hyaline.

The *peridium* is thin, white, and composed entirely of a dense, pliant weft of the terminal, slender branches of the radiating mycelium. The terminal branchlets are 3–5 $\mu$ in diameter at the base and taper out to a very slender point 1 $\mu$ or less in diameter. The walls are much thickened, so that the lumen of these narrow branchlets is nearly closed, quite so toward the apex. Many of these slender branchlets are free above the surface and give to the peridium a minutely tomentose, felt-like surface. Many of these branchlets arise very close together, and then are more or less dichotomously branched at a distance, a peculiarity often quite characteristic of the stouter internal mycelium.

*Internal mycelium and hold-fast.*—The internal mycelium has a general radial direction from the basal depression, diverging in all directions toward the peridium. The main hyphae are 12–15 $\mu$ in diameter. The branching is di- or trichotomous, or 4 to 5 or more branches arise close together, their point of origin often suggesting a ganglion-like enlargement of the parent hyphae from which the branches radiate. The course of the hyphae is more or less sinuous.

No cross walls have been observed, except in the progametes after copulation. The nuclei are minute, very numerous and lie in the peripheral granular cytoplasm. There is a nuclear membrane and a large nucleolus (? karyosome). The fruit bodies are quite firmly attached to the living sphagnum leaves, but the mycelium does not appear to be parasitic, although short haustoria have been seen penetrating the cell. The hold-fast is a rather compact lattice-like layer of mycelium forming a kind of "sole," very closely applied to the surface of the leaves, from which here and there the short haustoria arise. The fungus is probably nourished by organic and mineral solutions carried by the sphagnum from the water of the humus substrate in the capillary stream so well provided for in the peat mosses.

*Conjugation of the progametes.*—While there is a great resemblance in the process of conjugation and in the formation of the resting zygote of *Endogone sphagnophila* to the situation in *E. lactiflua*, the details of the process are quite different in the two species. The progamete branches lie nearly or quite parallel. In a few cases where they have been observed just prior to conjugation they do not appear to be differentiated from ordinary stout vegetative branches, except that the cytoplasm is more dense and abundant. They do not appear to be enlarged or clavate. In fact many of the vegetative branches are clavate and sometimes they are in pairs lying closely side by side, but in no case have I been able to determine with certainty that such branches are progametes. The progametes also appear to be undifferentiated before conjugation. They conjugate by lateral contact of their walls at the tip. Immediately after contact the progametes begin to swell into a clavate or fusoid form, and the wall at the point of contact is resorbed for some distance, thus forming a broad communicating area where the cytoplasm of the two merges. During the enlargement one of the gametes frequently becomes larger than the other. The cytoplasm is very dense and fills the distal portion of the progametes, while in the proximal direction the cytoplasm is less abundant and lies chiefly in a peripheral zone next the wall. A cross wall is now laid down in each progamete a short distance behind the broad communicating pore, separating the gametangia from the stalks or suspensors.

*Formation of the resting spore or resting zygote.*—At the time of conjugation and resorption of the contact wall the conjugating gametangia resembles the same stage of conjugation in *Eremascus fertilis*. The zygote is not formed by the enlargement of the copulating gametangia as in the majority of the Mucorales, but the young zygote begins to grow at once in an apical direction. Sometimes the origin

of the young zygote is symmetrical in relation to the two gametangia, that is, the tip of each gametange shares equally in the growth. In other cases the new growth arises more from one than the other, usually from the larger one where they are unequal in size. More rarely does the new growth arise entirely from the larger gametange, but the communication is so broad that both gametangia remain in direct communication with the contents of the new growth. This new growth, or progressive zygote, enlarges to a broadly elliptical structure, 35–60 x 30–45 $\mu$. It stands on the two supporting gametangia, and the protoplasm of the gametangia and new zygote is continuous. When the new zygote has reached its full size the protoplasm in the gametangia withdraws and merges with that in the zygote. A new wall is now laid down inside of the primary zygote membrane. At first thin, it increases in thickness, forming a white, stratified, cartilaginous layer around the protoplasm, thus cutting off communication with the empty gametangia. The two stalks which support the mature resting zygote are not simply the suspensors, but the empty gametangia plus the suspensors. The resting zygote is nearly filled with very minute rounded or slightly irregular hyaline bodies, which appear to be fat bodies, since they stain red with Sudan III. There is a rounded clear space in the center, *i. e.*, in the middle of the long axis, but in some zygotes it lies on one side next the wall. In fixed and stained material the center of this vacuole (?) appears to be occupied with a coarsely granular body or mass of minute bodies.

*Cytology of conjugation and zygote formation.*—The number of nuclei in the gametangia is variable, probably from five to ten or more in each. No evidence of nuclear division in the progametes or gametangia has been observed, and no evidence has been seen of a selection of gamete nuclei. Nor does it appear that there is any nuclear degeneration in the progametes before the formation in the cross wall which differentiates the gametangia. Following this stage nuclei in the suspensors may degenerate. The cytoplasm in the gametangia is so dense and stains so deeply that it is sometimes difficult to differentiate the nuclei. When the stain is not too deep the nuclei are clearly seen. They are considerably larger than the vegetative nuclei, the increase being due to growth. There is a nuclear membrane, a clear court in which are sometimes visible a few delicate threads, perhaps portions of the linen or chromatin. There is a prominent central, spherical, nucleolus or karyosome, which stains red with Flemming's triple stain, dark with iron haematoxylon. The nuclei are disposed in the cytoplasm of the gametangia without order. They gradually migrate into the new zygote, as it is formed, along with the cytoplasm.

In the young zygote the cytoplasm is at first dense and rather

homogeneous as in the gametangia. But as the new zygote enlarges the cytoplasm becomes coarsely reticulate. The strands are coarse and with an irregular outline. They radiate irregularly from the center to the periphery and anastomose by irregular branches, forming a large meshed network the strands of which are coarser in the central region, thinner toward the periphery. During the early stages of development of the young zygote the nuclei appear to have a general distribution, but have not been observed near the periphery. As the zygote approaches its full size the nuclei occupy the more central region, being distributed from the center to a zone half way, or a little more, to the periphery. Sometimes the centralization is more marked. At this stage there appears to be a differentiation of the cytoplasm, or rather, the appearance of a clear homogeneous plasma occupying the nuclear region and in which the nuclei die. When the nuclei are strongly centralized, the homogeneous plasma appears to form a single large central area. When they are more widely distributed, the homogeneous plasma is separated into several areas, each area containing several nuclei. During all this period the coarsely reticulate cytoplasm occupies the entire zygote.

A provisional suggestion as to the function of this homogeneous plasma is that it serves as a medium for the freer movement of the nuclei than can take place in the coarsely reticulated cytoplasm; or the homogeneous plasma may actually serve to move the nuclei to a certain extent, possibly bringing them into closer proximity in the center and later carrying them into the peripheral zone. In this central region the nuclei are generally in pairs and the two nuclei of a pair appear to fuse. This fusion of paired nuclei in the zygote corresponds with the fusion of paired nuclei in certain of the Mucorales as described by Gruber (1901) in *Sporodinia grandis*, Dangeard (1906) in *Rhizopus nigricans*, and Moreau (1911–1913) in *Rhizopus nigricans* and species of *Zygorhyncus*. The fusion of the nuclei of a pair is suggested by the fact that they are found close together, sometimes the nuclear membranes in contact, again an elongated nucleus (? fusion) with one membrane and this constricted between the two nucleoli, and further two nucleoli surrounded by one membrane which is not constricted. Of course these relations might be the result of nuclear division, but no figures appear at this stage which suggest a division of the nuclei.

In a later stage of development the coarse reticulum of the cytoplasm disappears. The cytoplasm becomes more homogeneous. The nuclei appear to occupy a zone about half way between the center and periphery. Figures are present which suggest a division of the nuclei at this stage, for the nuclei are often two to three times

longer than broad, presenting the appearance of rods, deeply stained, lying in a peripheral zone of the cytoplasm.

The material on which this cytological study was made was not as well fixed as it might have been. The peridium of the fruit bodies is very dense and tough, not permitting the rapid penetration of the fixing fluids. Then in the later stages of zygote formation the thick cartilaginous wall of the resting zygote very likely offers great resistance to the penetration of the fluids. An attempt will be made to collect more material during the present season, when the fruit bodies will be cut open before placing them in the fixing solutions, and also it is hoped that younger stages of development may be secured.

Up to the present time no one has succeeded in germinating the resting zygotes of any species of *Endogone*. Link (1809), Fischer (1897, p. 121, 124) and Bucholtz (1912) have described sporulation in the "resting spores" (azygotes) of *Endogone pisiformis*, a parthenogenetic species. In this species the wall of the resting spore is only slightly thickened. According to Fischer and Bucholtz the content of the resting spore is gradually divided into angular areas which round up and form a number of large elliptical spores inside the wall of the resting spore (or ? sporangium). Their study was not made on living material, but on specimens preserved for several years. There was no intersporal substance or epiplasm.

I have made several attempts to germinate the resting zygotes of *Endogone sphagnophila*, but thus far without success. The first attempts were made in December, 1916, with material kept on sphagnum under cover of a bell jar in the shade on the north side of a building. The cultures were made by tearing out mats of mycelium with the resting zygotes in a thin layer of water on glass slides which were kept in moist chambers. The cultures were examined day by day for a period of two weeks. These cultures were then allowed to remain out of doors on a window ledge with a southern exposure until the middle of January, 1917, when they were brought inside and again examined daily for a period of a week. During the latter part of March and early in April, 1917, fresh cultures were started from the same source, *i. e.*, from fruit bodies kept on sphagnum out of doors, where they were subject to freezing and thaw. Thus far (Apr. 17, 1917) there has been no evidence of germination, although the great majority of the zygotes appear to be alive and in good condition. A few of the zygotes, however, appear to be dead. In many of these the content is divided into irregular bodies. Others are filled with elliptical or globose bodies, in some instances with intersporal substance. These bodies, some of them, at least appear to be spores,

but I am strongly inclined to believe that they are spores of some parasite.

## Relationships of Endogone

The coenocytic mycelium with no true cross walls, except those which separate reproductive organs from the mycelium, with the formation of resting zygotes soon after the conjugation of gametangia, are phycomycete characters. The method of conjugation of equal or slightly unequal gametangia indicates a closer relationship with the Zygomycetes than with the Oomycetes, although in *Endogone lactiflua* the content of the small gametange, or antherid, flows into the larger one which is comparable to the oogone. In *Zygorhyncus* the two gametangia are very unequal in size, but the zygote is formed within and includes all of both gametangia, a strictly zygomycete feature. In *Conidiobolus* the gametangia are of very unequal size, and are worthy of being distinguished as antherid and oogone. The content of the antherid passes into the oogone within which the zygote is formed. In *Basidiobolus*[2] also there is a supplying gametange and a receiving one, but other features of these genera, especially conidial formation, show such a close relation to *Empusa* that they are generally regarded as members of the zygomycetes with a leaning toward the oomycetous type of fructification, but not having reached the characteristic feature of egg differentiation in the oogone. *Endogone* departs from the usual type of zygote formation present in the zygomycetes. The zygote is an outgrowth from the conjugation point of the gametangia (*E. sphagnophila*), or from the larger gametange (*E. lactiflua*, rarely in *E. sphagnophila*). A similar situation, however, is present in *Piptocephalis freseniana* and in *Empusa* (*Entomophthora*) *fresenii*, where the zygote is an outgrowth of the point of conjugation much as in *Endogone sphagnophila*. In *Empusa occidentalis*, *echinospora*, *sepulchralis*, etc., the zygote is an outgrowth of one of the gametangia, a situation similar to that in *Endogone lactiflua*, or sometimes it arises from the point of conjugation in these species of *Empusa*.

In the selection of a single sex nucleus in each gametange, *E. lactiflua* presents a situation similar to that in the Peronosporales, though there is no differentiation of ooplasm and periplasm in the oogone of *Endogone lactiflua*, as there is in the Peronosporales. In *E. sphagnophila* there is no sex selection of nuclei in the gametangia so far as we can determine, for all of the nuclei without manifesting any differentiation pass with the cytoplasm into the new outgrowth where the zygote is formed. The nuclear behavior in the zygote has not yet been made entirely clear. The present evidence suggests that

[2] *Basidiobolus* by some is placed in a distinct family.

there is first a nuclear fusion in pairs, perhaps some of the nuclei degenerating. If this is confirmed the situation in *E. sphagnophila* agrees in this respect with that in the Mucorales. It appears also that later, when the nuclei lie in a peripheral zone, they undergo at least one division. At the present stage of the investigation the possibility is not excluded that fusion of nuclear pairs does not occur. It is also possible that after the division of the nuclei in the peripheral zone of the zygote all but two may degenerate, the two selected ones later uniting to form the fusion nucleus. This would bring *E. sphagnophila* more nearly in line with the process in *E. lactiflua* as described by Bucholtz, the selection of the sex nuclei being postponed to a late period in *E. sphagnophila*. I do not think, however, that this is the case, but am inclined rather to believe that there is multinuclear fusion in pairs,[3] similar to that which takes place in the Mucorales as described by Gruber (1901) in *Sporodinia*, by Dangeard (1906) in *Sporodinia*, and by Moreau (1911–1913) in *Rhizopus*, *Zygorhyncus* and *Sporodinia*. That in certain species of *Endogone* there is fusion of but one pair of sex nuclei in the zygote, while in other species there may be fusion of several pairs of sex nuclei, is not incomprehensible in view of the nuclear process in fertilization in *Cystopus* (See Stevens 1899, 1901), where in *C. bliti* and *portulacae* there are fusions of many pairs of sex nuclei in the egg, while in other species there is fusion of a single pair of sex nuclei.

There is another feature in *E. lactiflua* which is paralleled in certain of the Zygomycetes. This is the hyphal envelope which encloses each zygote. Crude tendencies to such an envelope are present in *Phycomyces* and *Absidia* of the Mucorales and in *Empusa rhizospora* of the Entomophthorales (Thaxter, 1888), while in *Mortierella* there is a well-developed envelope. In no other species of *Endogone*, however, is such an envelope around each zygote known, not even a rudimentary one. In this respect *E. lactiflua* represents a more advanced stage of evolution, which is manifested also in the origin of the resting zygote as a distinct outgrowth of the larger gametange. This species may possibly represent the type of a distinct genus, so widely does it depart in these two respects from all the other known species.

There is another feature, however, in which *Endogone* departs widely from any other known phycomycete. The mycelium and numerous zygotes ("resting" spores or "sporangia" in the parthenogenetic species) are united into a compact and distinct fruit body, or

[3] According to Leger (1896) in *Sporodinia grandis*, and according to Miss McCormick (1912) in *Rhizopus nigricans*, all nuclei but two degenerate in the zygote, but this has not been confirmed.

zygocarp with a definite and well-developed peridium. This represents a distinct progression in development over all other phycomycetes, a cephalization of zygotes into a complex fruit body.

The heterogamous character of the gametangia of *Endogone lactiflua* and the selection of a single gamete nucleus in each are oomycete features. But the lack of differentiation in the cytoplasm in the oogone, or gametangia, is a zygomycete feature. For these reasons Bucholtz[4] interprets *Endogone* as occupying an intermediate position between the zygomycetes and Oomycetes, but constituting a distinct group, the Endogoneae.[5] He probably regards this intermediate position as simply taxonomic, not phylogenetic.

## Relation of Endogone to the Ascomycetes

*Endogone* has been shifted in all the three great divisions of the fungi. It was first placed in the Basidiomycetes near *Rhizopogon* by Link (1809) who was followed by Fries (Syst. Myc. **2**, 295, 1822). For a long time it has remained in the Ascomycetes, being placed in the Tuberaceae by Vittadini (1831), by Tulasne (1857), by Saccardo (Syll. Fung. **8**, 905, 1889). Schroeter (1889) placed *Endogone* with some uncertainty in the Order Protomycetes, the highest order of the Phycomycetes. He was followed by Saccardo (Syll. Fung. **14**, 829, 1899), and it is significant that the genus *Protomyces* has by many students been placed in the Phycomycetes. In 1897 Schroeter, while still retaining *Endogone* in the Protomycetaceae, transferred the group to the Hemiascineae.

Until we know the morphological and cytological phenomena in connection with the germination of the resting zygotes of *Endogone* we cannot say with any degree of precision what relation it bears to the Ascomycetes, nor how near that relation is. It appears quite probable that *Endogone* does bear an interesting relation to the Protoascomycetes. If the resting zygotes germinate fructificatively with free cell sporulation, somewhat as occurs in *Dipodascus* or *Protomydes*, its relation to the Protoascomycetes would be very clear. The question would then arise whether with its coenocytic mycelium it should be placed on a level with *Dipodascus* or just below it, representing the highest level of the Phycomycetes. Even if the germination phenomena should prove to be of the phycomycete type, *Endo-*

[4] He describes two large nuclei in the zygote of *E. ludwigii*, a sexual species.

[5] The genus has been considered for a long time by a number of students to represent a distinct family. Fries (Summa Veg. Scand. 1849) proposed the family Endogonaceae and in view of Bucholtz's studies it is interesting to note that Schroeter in 1889 placed it along with Protomyces as the highest member of the Phycomycetes.

*gone* would still represent the nearest approach of the phycomycete type to the ascomycete type. The method of conjugation of the gametangia, and the growth of the zygote, in *Endogone sphagnophila*, is surprisingly like that in *Eremascus fertilis* and in *Dipodascus*. Even without the knowledge of germination of the resting zygotes in *Endogone*, the genus seems to offer more of the characteristics of a prototype of the Protoascomycetes (and perhaps also of the Uredinales) than any other known phycomycete.[6] *Endogone* presents additional strong evidence of the phycomycete ancestry of the Ascomycetes.

All of the evidence considered, it appears to point more strongly to the zygomycete alliance as the source of the primitive ascomycete stock, rather than to the oomycete alliance. In the oomycetes the sexual organs and the processes of fertilization have become very highly specialized. The sexual organs are highly differentiated; one or more distinct eggs are differentiated in the oogone, in many cases the protoplasm being differentiated into ooplasm and periplasm; while a special fertilization tube from the antherid penetrates the oogone, or in a rare and specialized case a motile sperm enters the oogone through a pore (*Monoblepharis*).

In the zygomycetes the sexual organs have retained a simple and generalized condition. Copulation is by pore formation with merging of the content of the gametangia. In most cases the gametangia are equal and the zygotes mature *in situ*, within and comprising all of both gametangia. Progression in the zygomycetes, however, is manifested in five directions.

1. In a tendency to differentiation in size of the gametes.

2. A tendency to differentiation of the gametangia in function, the larger one becoming the receiving gametange, the oogone, but without differentiation of content into egg and periplasm; the other serving as the supplying gametange, antherid (*Conidiobolus utriculosus*, *Basidiobolus ranarum*, *Dispira americana* Thaxter, 1895, *Endogone lactiflua*, etc.).

3. The progressive tendency shown in the germination, or outgrowth, of the young zygote immediately after fusion from the copulation point, or from one of the gametangia, the ripe zygote being formed outside the gametangia, not within them according to the typical process. The tendencies in this direction appear at different levels in the zygomycete alliance. Examples are *Piptocephalis freseniana*,

[6] The following forms among the phycomycetes have been suggested as prototypes of the ascomycetes. The Peronosporales by de Bary (1881) for the usual ascomycete type, *Piptocephalis* for the *Eremascus* type; *Myzocytium* and *Protascus* by Dangeard (1903–06, 1910), *Cystopus* by Lotsy (1907) and *Monoblepharis* by Nienburg (1914).

*Empusa* (*Entomopthora*) *fresenii*, *Empusa rhizospora*, *sepulchralis*, etc., *Endogone sphagnophila* and *lactiflua*.

4. Progression in the direction of selection of sex nuclei. In *Endogone lactiflua* one sex nucleus is selected from among all the potential ones in each gamete. This illustrates how the situation in *Dipodascus*, *Eremascus fertilis* and in *Endomyces* has arisen. This situation is presaged in some of the lower zygomycetes in the degeneration of some of the gamete nuclei in *Rhizopus*, *Sporodinia* and *Zygorhynchus*, if we may accept the account by Moreau (1911, 1913). In *Endogone sphagnophila* there are many potential and many functional nuclei in the gametangia and these are carried on into the young germinating, or progressive zygote. This type illustrates a situation which has been retained in those ascomycetes with multinucleate gametangia as in *Monascus*, the Gymnoascaceae, *Ascodesmis*, *Pyronema*, etc.

5. The postponement or moving forward of the moment of nuclear fusion from the gametangia to the new outgrowth, or progressive zygote. The examples are the same as those given in paragraph 3. In the zygomycete alliance *Endogone lactiflua* represents the most progressive stage in these directions of any known species, unless *Dipodascus* should be regarded as a phycomycete. The sex pair of nuclei is organized by the migration of the antheridial nucleus into the oogone. The pair then migrates into the new outgrowth where the sex nuclei lie side by side in the resting zygote, or fuse, in one variety. As Bucholtz (1912) points out there is wanting here only the conjugate division of the nuclear pair to parallel the situation in the ascogenous hyphae of the true ascomycetes.

From the situation reached by progression in these directions, by members of the zygomycete alliance, there is but a small gap over which to bridge in reaching the protoascomycetes. The principal steps may be indicated as follows:

1. Free cell sporulation of the progressive zygote of *Endogone*. This alone would place this zygote in the category of a generalized ascus, and *Endogone* would become a fit member of the protoascomycetes. Intersporal substance present in the sporangium of some phycomycetes during sporulation may possibly presage typical free cell sporulation. Other steps toward the true ascomycetes are indicated in the following.

2. The omission of a period of rest by the progressive zygote and the immediate free cell sporulation of the same. This step alone would reach the level of *Dipodascus*, *Eremascus*, *Endomyces magnusii*, etc.

3. Vegetative growth of the zygote and postponement of free cell

sporulation until the second or third cell of the new growth, would carry the zygote to the level of that in *Sphaerotheca*, in the true ascomycetes.

4. Vegetative growth of the zygote with splitting of the same by branching, thus multiplying the terminal branches of the zygote in which free cell sporulation takes place, carries the zygote to the level of *Pyronema*, *Monascus*, etc., in the true ascomycetes.

5. Organization of a fruit body by formation of a peridium of the interwoven terminal branches of the mycelium. This is already realized in the complex zygocarp of *Endogone*, the peridium being on a level with that in the Gymnoascaceae.

6. Organization of a peridium by enveloping hyphal branches of the type in *Monascus*, the *Erysiphaceae*, *Aspergillus*, etc. This feature is already realized in the simple zygocarp of *Endogone lactiflua*.

## Relation of the Zygotes and Azygotes in Endogone

Several species of *Endogone* are parthenogenetic (*E. macrocarpa*, *microcarpa*, *pisiformis*, etc.), yet the "resting spores" are similar to the resting zygotes of *E. sphagnophila*, *ludwigii*, etc., in all other respects so far as known at present, with the exception of the number of nuclei in the resting stage. According to Bucholtz the zygotes of the sexual species, *E. lactiflua* and *E. ludwigii*, are binucleate in the resting stage, while the azygotes of *E. pisiformis*, *macrocarpa*, *microcarpa*, etc., are multinucleate. However, the zygotes of the sexual species *E. sphagnophila*, are probably multinucleate in the resting stage. It is very probable that at the time of germination the zygotes of *E. lactiflua* and *E. ludwigii* become multinucleate by successive divisions of the fusion nucleus. It is, therefore, very likely that the phenomena of germination, whatever the type of germination is for *Endogone*, is the same in the sexual and parthenogenetic species. It is quite evident that the branch in which the azygote is formed is the morphological equivalent of a gametange, just as the sporangia and gametangia of *Monoblepharis*, *Saprolegnia*, etc., are morphological equivalents. If there were sex differentiation among the nuclei of the zygotes followed by fusion, then the azygotes would be strictly homologous with the zygotes, in fact they would be zygotes. Bucholtz (1912) regards the simple zygocarp of *Endogone lactiflua* as homologous with the germ sporangium (carposporangium) of the Mucorales and Peronosporales. In a certain degree this is true, but it is also homologous with the zygote of the Mucorales and Peronosporales. In the Mucorales the germ sporangium is external to the zygote while in the Peronosporales it is internal. The germ sporangium of *Endogone* is not known, it may be internal or external to the zygote. The zygote

of *Endogone* presages the beginning of a new structure, not more so than does the zygote of *Piptocephalis* and of certain species of *Empusa*, etc., but it is still homologous with the zygote of the other phycomycetes.

In the Mucorales, aside from the meiotic divisions of the fusion nuclei, the process of sporulation in the germ sporangium (sporangium formed on germination of the zygote) is the same as that in the "asexual" sporangium. The germ sporangium and the asexual sporangium are morphological equivalents. The germ sporangium is not a new morphological structure, though the zygote and early stages of its germination presage the origin of a new morphological structure. Historical experience turns it quickly back into the well-worn trail. The very simple primordium of the new structure does not mark out a new path until the accumulation of new experiences, together with environment, provide the threshold for progress to the new structure.

If nuclear fusion does not occur in the azygotes of *Endogone* then the chromosome history, so far as we know, would run from generation to generation without change. The two situations may be represented thus:

| | | | |
|---|---|---|---|
| Sexual species of *Endogone*. | IX → IX → IX → IX<br>Mycelium and gametangia | ↗ 2X ↘<br>zygote | IX → IX etc.<br>spores, mycelium. |
| Parthenogenetic species of *Endogone*. | IX → IX → IX → IX<br>Mycelium and gametangium | → IX →<br>azygote | IX → IX etc.<br>spores, mycelium. |

As sporulating organs the zygote and azygote (or germ sporangium of the same) of *Endogone* are homologous structures. The true asexual sporangium has been eliminated. Likewise, in the protoascomycetes, where the threshold from the phycomycetes has been crossed, the zygote ("germ sporangium," a generalized ascus) of *Dipodascus*, and the azygote ("germ sporangium," "generalized ascus") of *Ascoidea*, as sporulating organs are homologous structures. *Ascoidea* is probably parthenogenetic, the "generalized ascus" being a transformed gametangium. Free cell sporulation occurs in both genera. This interpretation of the relation of the free cell sporulating organs of *Dipodascus* and *Ascoidea* is supported by the situation in *Eremascus fertilis* and *Endomyces magnusii* where the ascus is in some cases of sexual origin, in others of parthenogenetic origin, a single gametange becoming the ascus. *Endogone*, with several sexual species having sexually produced sporulating organs (zygotes), and other species with parthenogenetically produced sporulating organs (azygotes), is interesting in that it illustrates the homology of these structures, and suggests how the parthenogenetic sporulating organs (generalized asci) of *Ascoidea*, *Protomyces*, etc., may have arisen. It is interesting

to note that the forms with parthenogenetic asci, generalized or not, were not endowed with potentialities of progress, nor with the evolution of any important lines. They have made practically little progress and are few in number. On the other hand, those forms with sexually produced asci, even though the sexuality be of a very greatly reduced type, were endowed with great potentialities as evidenced by the large group of Euascomycetes with high specialization, and great divergence of character in several different series.

## Technical Description

*Endogone sphagnophila*[7] n. sp. *Plants* (zygocarps), 2–4 mm. in diameter, pulvinate, reniform, plain or subcerebriform with two to three low lobes or convolutions, orange yellow when mature, *Peridium* white, submembranous, tough, of interwoven coenocytic, profusely branched hyphae, minutely tomentose or downy from free, terminal, very slender branchlets, 4–5 $\mu$ at base, 1 $\mu$ or less at the tips. *Mycelium* of the zygocarp 10–15 $\mu$ in diameter, coenocytic, stout, non-septate, branched in a dichotomous, or trichotomous manner, or several branches springing from enlargements, radial, the terminal branches interlacing to form the peridium. *Progametes* equal. *Gametangia* separated from mycelium by a cross wall, equal or usually slightly unequal, multinucleate. "*Resting spores*" (zygotes) formed as an outgrowth from the conjugation point of the gametangia, or more rarely from the larger one, one resting spore formed in the primary zygote membrane from each pair of gametangia, elliptical to oval, rarely irregular, with orange yellow content and a thick, white, stratified cartilaginous wall, 35–60 x 30–45 $\mu$, germination unknown.

On sphagnum in a ravine in region of Seventh Lake, Fulton Chain, Adirondack Mts., New York, July 1916, Aug. 1917; and in Cranesville moor, Western Maryland, Sept. 1917 (rarely on other mosses or on dead twigs). Thaxter (Bot. Gaz. **24**: 12, 1897) reports it on sphagnum in Maine.

*Latin diagnosis.* Pulvinatis, reniformibus, subcerebriformibus, aureis, 2–4 mm.; peridiis albidis submenbranceis, lentis, floccosis intertextis, tomentosulis; myceliis glebae 12–15 $\mu$, radiatis, dichotomis vel trichotonis vel plurichotomis, ramulis terminalibus peridium formantibus; sporis orientibus ab gametangiis copulantibus, ellipsoideis vel ovalibus, maximis, 35–60 x 30–45 $\mu$, plasmate aureo. Hab. on sphagnum, Adirondack Mts., New York, and in Maine and Maryland.

## LITERATURE CITED

**Atkinson, Geo. F.** Phylogeny and Relationships in the Ascomycetes. Ann. Mo. Bot. Garden 2: 315–376. Figs. 1–9. 1914.

[7] Closely related to *E. ludwigii* Bucholtz, but this species is subterranean with a prominent germ pore in the thick wall of the zygote and the nuclei are reduced to two which fuse at maturity.

**de Bary, A.** Untersuchungen über die Peronosporeen und Saprolegnieen und die Grundlagen eines natürlichen Systems der Pilze. In de Bary und Woronin, Beitr. z. Morph. u. Physiol. d. Pilze **4**: 1–145. Pls. 1–6. 1881.

**Brefeld, O.** Die Hemiasci und die Ascomyceten. Untersuch. Gesammtg. Myk. **9**: 1–156. Pls. 1–3B. 1891.

—— Ascomyceten II. Ibid. **10**: 157–378. Pls. 4–13. 1891.

**Bucholtz, F.** Beiträge zur Kenntnis der Gattung Endogone Link. Beihefte Bot. Centr. **29**: 147–225. Pls. 3–10. 1912.

**Dangeard, P. A.** Recherches sur le développement du périthèce chez les Ascomycetes. Première partie. Les ancetres des champignon superieurs. Le Botaniste **9**: 157–303. Pls. 1–18. 1903–1906.

—— La fecondation nucléaire chez les Mucorinées. C. R. Acad. Sci. Paris. 1906.

—— Recherches sur le développement du périthèce chez les Ascomycetes. Le Botaniste **10**: 1–385. Pls. 1–91. 1907.

**Fischer, E.** Tuberaceen und Hemiasceen, in Rab. Krypt. Fl. 2nd Auf. Die Pilze 5th Abt. 1–151. 1897.

—— Pilze in Handwörterbuch der Naturw. **7**: 880–929. 1912.

**Gruber, E.** Ueber das Verhalten der Zellkerne in den Zygosporen von Sporodinia grandis. Ber. deuts. bot. Ges. **19**: 51–55. Pl. 2. 1901.

**Léger, M.** Recherches sur la structure des Mucorinées. Paris, Poitiers. 1896.

**Link.** O. B. S. Pl. nat. **3**: 33. 1809.

**Lotsy, J. P.** Vorträge über botanische Stammesgeschichte **1**: I–IV and 1–828. F. 1–430. 1907.

**McCormick, F. L. A.** Development of the Zygospore of Rhizopus nigricans. Bot. Gaz. **53**: 67–68. 1912.

**Moreau, F.** Deuxieme note sur les Mucorinées. Fusions de noyaux et dégenerescence nucléaire dans la zygospore. Soc. Myc. France Bull. **27**: 334–341. 1911.

**Moreau, F.** Sur la reproduction sexuée-de Zygorhynchus moelleri Vuill. C. R. Soc. Biol. **73**: 452–455. 1911.

—— Les phénomènes intimes de la reproduction sexuelle chez quelques Mucorinées hétérogames. Soc. Bot. France Bull. **58**: 618–623. 1911.

—— Une nouvelle Mucorinée héterogame Zygorhynchus dangeardi sp. nov. Soc. Bot. France Bull. **59**: LXVII–LXX. 1912.

—— Recherches sur la reproduction des Mucorinées et quelques autres thallophytes. Thèses presentées a la Fac. Sci. Univ. Paris 1–136. Pls. 1–14. 1913.

—— Les karyogamies multiples de la zygospore de Rhizopus nigricans. Soc. Bot. France Bull. **60**: 121–123. 1913.

**Schroeter, J.** Cohn's Krypt. Fl. Schlesien. $3^1$: Pilze. Protomycetes. 257–260. 1886.

—— Hemiascineae in Engler & Prantl. Pflanzf. $1^1$: 143–149. 1894.

**Stevens, F. L.** The compound oösphere of Albugo bliti. Bot. Gaz. **28**: 149–176, 225–245. Pls. 11–15. 1899.

—— Gametogenesis and fertilization in Albugo. Bot. Gaz. **32**: 77–98, 157–169, 238–261. Pls. 1–4. F. 1. 1901.

**Thaxter, R.** New or peculiar American Zygomycetes. I. Dispira. Bot. Gaz. **20**: 513–518. Pls. 34. 1895.

**Tulasne, L. R. et Ch.** Fungi Hypogaei. Pp. I–XIX, 1–222. Pls. 1–21. 1851.

**Vittadini.** Monographie Tuberacées. 1831.

# A VEGETATIVE REVERSION IN PORTULACA

*(Abstract)*

A. F. BLAKESLEE AND B. T. AVERY, JR.

*Station for Experimental Evolution, Cold Spring Harbor, N. Y.*

A single dwarf individual was discovered in a bed of plants from commercial seed of *Portulaca grandiflora*. When the dwarf is selfed it throws all dwarfs. Some of the dwarf offspring produce reverting branches which differ from the dwarf stock upon which they are borne by having red, instead of green stems and by having longer internodes. The flowers on both dwarf stock and reverting branches are red. Selfed seed from the reverting branches produces both dwarfs with short internodes and normal plants with long internodes as well as occasional dwarfs that show reverting branches.

# THE FLORA OF THE AMERICAN VIRGIN ISLANDS

N. L. BRITTON

*New York Botanical Garden*

The islands St. Thomas, St. Jan and St. Croix recently purchased by the United States from the kingdom of Denmark, are situated to the east and southeast of the island of Porto Rico. My interest in their flora was first aroused by the proximity of the Virgin Islands archipelago to Porto Rico, both the Porto Rican islands Culebra and Vieques being parts of the archipelago. I therefore took occasion in 1913, accompanied by Dr. J. N. Rose and with the help of Mrs. Britton, Miss Delia W. Marble, and Dr. J. A. Shafer, to explore St. Thomas and St. Jan quite thoroughly, and Dr. Rose made collections on St. Croix, while we were engaged in studying the cacti of the West Indies.[1] In 1901, I had made a brief visit to St. Croix, with Mr. John F. Cowell.[2]

The islands are all hilly, there being very little level land on either St. Thomas or St. Jan, but more on St. Croix. The rocks are mostly of plutonic origin, but there is some limestone on St. Croix and locally other stratified rocks occur. The highest elevation is about 500 meters (1,550 feet), on The Crown of St. Thomas.

There is but little natural forest remaining on any of the islands, and what there is is confined to the hilltops in a few places. Reforestation is the crying need of the new possession, and it will be highly discreditable to the United States if this subject is not immediately taken in hand. Most of the higher parts of all three islands are not available for any but forest products and the supply of wood for fuel needs to be increased and the rainfall conserved by a forest cover, for most of the rain now runs off immediately. This destruction of the forest has doubtless eliminated a good many species from the original flora of the islands.

The principal literature of the botany of the islands is as follows:[3]

**H. West.** "Bidrag til Beskrivelse over Ste Croix, med en kort udsigt over St. Thomas, St. Jean, Tortola, Spanishtown og Crabeneiland." Kiöbenhavn. Pp. 363. 1793. [German edition pp. 274, Copenhagen 1794.]

West enumerates and partly describes 542 species, of which 111 were culti-

[1] Jour. N. Y. Bot. Gard. 14: 99–109.

[2] Jour. N. Y. Bot. Gard. 2: 166.

[3] See also citations in the chapters on Hepaticae, Fungi and Algae.

vated, mainly of St. Croix, a few from St. Thomas and St. Jan. Some of the descriptions are by Vahl. A number of the plants listed have not been observed on St. Croix by subsequent collectors and some of them are obscure. The author was rector of a school at Christiansted. The book is very rare. I am indebted to The New York Public Library for a photostat copy.

**André Pierre Ledru.** "Voyage aux îles de Ténériffe, La Trinité, Saint-Thomas, Sainte Croix et Porto Ricco, exécuté par ordre du gouvernement français, depuis le 30 septembre 1796 jusqu' au 7 juin 1798, sous la direction du capitaine Baudin, pour faire des recherches et des collections relatives a l'histoire naturelle; contenant des observations sur le climat, le sol, la population, l'agriculture, les productions de ces îles, le caractère, les moeurs et le commerce de leurs habitants." Ouvrage accompagné de notes et d'additions par M. Sonnini. Avec une très belle carte gravée par J. B. Tardieu d'après Lopez. Paris. 2 vol. 1810.

Ledru was the botanist and Anselme Riedlé the gardener of an expedition sent out by the Paris Museum of Natural History 1796–1798. Unfortunately, many of the specimens attributed to St. Thomas were in all probability collected on Porto Rico. Many living plants were brought back to the Jardin des Plantes. The botanical parts of the report are general and not extensive.

**D. F. L. de Schlechtendal.** "Florula insulae Sti. Thomae Indiae occidentalis." Linnaea, **3**: 251–276; **4**: 78–93; **5**: 177–200, 682–688; **6**: 722–772. 1828–1831.

About 400 species are enumerated. The plants were collected by C. A. Ehrenberg, a merchant, in the years 1827 and 1828. The records are annotated and there are some descriptions.

**Henry Krebs.** "Catalogue of plants found on the island of St. Thomas, W. I." 1852. [In John P. Knox: A historical account of St. Thomas, W. I., with its rise and progress in commerce, missions and churches, climate and its adaptation to invalids, geological structure, natural history and botany. New York.]

Over 1,200 plants are enumerated alphabetically, including many in cultivation and some algae. Many of the records can not now be substantiated. Krebs had previously published an account of the geographic distribution of the Flora of St. Thomas.

**J. P. Knox.** "Catalogue des plantes qui naissent spontanément dans l'isle de Saint-Thomas." 1857. [Memorie della r. Acad. di Torino, II, **16**: lxxvi–lxxxix.]

This is essentially the same document as the preceding.

**H. F. A. Eggers.** "St. Croix's Flora." Vidensk. Meddel. Kjøbenhavn. Pp. 33–158. 1876.

Baron Eggers was a Danish official on St. Croix from 1869 to 1874, and made extensive botanical collections. He records 738 species, with annotations.

**H. F. A. Eggers.** "Flora of St. Croix and the Virgin Islands, West Indies." Bull. U. S. Nat. Mus. 13. Pp. 133. 1879.

Baron Eggers was in command of Danish troops on St. Thomas during most of the period between 1874 and 1887, and visited St. Jan. In this catalogue he enumerates 881 indigenous or naturalized species, with annotations, and also records many of the plants in cultivation.

**H. F. A. Eggers.** "Supplement til St. Croix's og Jomfruøernes Flora." Vidensk. Meddel. Kjøbenhavn, pp. 11–21. 1889.

This work contains additional records to those previously published by the author.

**Otto Kuntze.** "Um die Erde." Pp. 514. Leipzig. 1881.

Dr. Kuntze visited St. Thomas in 1874, at the beginning of his extensive travels.

**Otto Kuntze.** "Revisio Generum Plantarum" 1: 2: pp. 1009. Leipzig. 1891.

The author records specimens collected by him on St. Thomas in 1874.

**F. Borgesen and Ove Paulsen.** "Om Vegetationen paa de Dansk-Vestindiske Øer." Botan. Tidsskr. Kjøbenhavn, 22: 1–114, *f.1–43*. 1898. [Reprint pp. 114.]

Mr. Borgesen visited the islands in 1892, and again in 1895–6, on his second trip accompanied by Mr. Paulsen. They made extensive collections, and listed six Spermatophytes as additions to the known flora. The document is mostly ecologic, and especially detailed as to the composition of the coastal vegetation. It was translated into French by Mlle. S. Eriksson and published in 1900 (Rev. Gen. de Bot. 12: 99–107; 138–153; 224–245; 289–297; 344–354; 434–446; 489–510). [Reprint pp. 108.]

**C. F. Millspaugh.** "Plantae Utowanae." Field Col. Mus. Bot. 2: 1–110; 113–135. *pl. 25*. 1900.

During the cruise of the yacht *Utowana*, December, 1898, to March, 1899, Dr. Millspaugh, botanist of the expedition, visited St. Thomas on January 17 and 18, 1899, and collected about 200 species, which are enumerated.

**C. F. Millspaugh.** "Flora of the Island of St. Croix." Field Col. Mus. Bot. 1: 441–546. Map. 1902.

Annotated list of 1,029 species, based especially upon the large collections made in 1895, 1896 and 1897 by A. E. Ricksecker and Mrs. J. J. Ricksecker, with records taken from Baron Eggers Flora. Mr. Ricksecker published a list of the species collected by him, pp. 4, not dated [1896]. Dr. Millspaugh has a chapter upon the botanical history of St. Croix.

**F. Borgesen.** "Notes on the Shore Vegetation of the Danish West Indian Islands." Bot. Tidsskr. 29: 201–259. *f.1–140*; *pl. 3–6*. 1909.

Mr. Borgesen made a third trip to the islands during the winter of 1905–1906, especially for algological studies. The paper is ecological, and supplementary to his earlier publications.

**E. G. Britton.** "Mosses of the Danish West Indies and Virgin Islands." Bull. Torr. Club 42: 1–8. 1915.

Mrs. Britton lists, with annotations, 28 species of Mosses, including 3 described as new; four of the plants enumerated were found only on Tortola.

**H. G. Brock, P. S. Smith, W. A. Tucker.** "The Danish West Indies, their Resources and Commercial Importance." 1917.

The United States Department of Commerce has recently published as Special Agents Series 129 (pp. 68, *figs. 1–8*), a valuable document in which the vegetable products of commercial value are discussed.

---

There are a very large number of records of plants from the islands in taxonomic monographs and lists of species by many authors.

As a literary curiosity record may be made of a manuscript list of the plants of St. Thomas, undated, arranged upon the Linnaean system of classification, preserved in the library of the New York Botanical Garden, presented some years ago by the late Dr. T. F. Allen.

General comments upon the vegetation are to be found in several books of travel.

The earlier collections of botanical specimens are practically all to be found only in the herbaria of the Old World. Perhaps the oldest

are those of Von Rohr and of Ryan, made about 1780, and preserved for the most part in the herbarium of the Botanical Museum at Copenhagen, where the most complete and extensive collections from these islands are to be found.

Prior to 1800 collections were made by L. C. M. Richard, Isert, West, Pflug, Ledru and Riedlé. During the nineteenth century the principal collectors were Benzon, Bertero, Ravn, Hornbeck, Ehrenberg, Breutel, Krebs, Oersted, Holton, Eggers, Krause, Warming, Borgesen, Paulsen, A. E. Ricksecker, Mrs. J. J. Ricksecker, Otto Kuntze and Millspaugh. Since 1900 collections have been made by N. L. Britton, Mrs. Britton, J. F. Cowell, Miss Marble, J. A. Shafer and J. N. Rose.

A collection made by Kirkman Finley in Trinidad was erroneously labeled as from St. Thomas, and many errors have been made in citing these specimens. A few plants collected by Kuntze in Porto Rico have been erroneously recorded as from St. Thomas, and many collected by Riedlé on Porto Rico have been similarly erroneously recorded. Conversely, some plants collected by Purdie on St. Thomas have been cited as Jamaican.

For the purposes of the following list of plants I have examined the literature and have studied the following series of specimens:

1. Duplicates of plants collected by Benzon, Hornbeck, Eggers and Paulsen, received by the New York Botanical Garden in exchange with the Copenhagen Botanical Museum.

2. The collection made by I. F. Holton on St. Thomas, preserved in the herbarium of Columbia University.

3. Dr. Otto Kuntze's St. Thomas plants, which came to the New York Botanical Garden as a part of his herbarium, presented by Mr. Andrew Carnegie.

4. The St. Croix collections made by Mr. Ricksecker and a portion of that made by Mrs. Ricksecker in the herbarium of the New York Botanical Garden and parts of the complete sets preserved in the herbarium of The Field Museum of Natural History.

5. Part of the St. Thomas collection made by Dr. Millspaugh.

6. The St. Croix collection made by Mr. Cowell and myself in 1900.

7. The collections made by Dr. Rose, assisted by Mr. Fitch and Mr. Russell on St. Croix in 1913.

8. The collection made on St. Thomas by Mrs. Britton and Miss Marble in 1913.

9. The collection made by Dr. Shafer and myself on St. Thomas, St. Jan and small adjacent islands in 1913.

Mrs. Britton has contributed the catalogue of the mosses, Dr. Evans that of the hepatics, and Professor Riddle that of the lichens.

Our knowledge of the fungi of the islands is but fragmentary and it is therefore deemed wise not to attempt an enumeration of them at this time; a mycological survey would doubtless reveal the presence of several hundred species. Dr. Howe has contributed a note on the algological collections and researches of Mr. Borgesen.

St. Thomas and St. Jan are two of the Virgin Islands, discovered by Columbus in 1493, and were so called to commemorate the young women who are fabled as having accompanied St. Ursula.

The Virgin Island group is usually regarded as composed of the following islands, proceeding from the west eastward, (1) Culebra, or Snake Island (Porto Rican); (2) St. Thomas, or San Thomé, and (3) St. John or San Jan; (4) Tortola, (5) Virgin Gorda, and (6) Anagada (British). Throughout this archipelago there are many islets and keys, and the marine views from the hills are among the most charming in America. If to the above mentioned larger islands we add (7) Jost Van Dyck, the next largest, a British island near Tortola, we have seven major Virgin Islands, eight if we include Vieques.

Tortola (British) is separated from St. Jan by little over a mile of water. The purchase from the Danish government thus brings our frontier close to that of the British Empire at another point.

Vieques, or Crab Island (Porto Rican), lies south of the axis of the archipelago, and is perhaps not properly a member of the Virgin Island group, although it is sometimes so considered.

These islands were originally inhabited by Arawak and Carib Indians. St. Thomas was colonized by the Dutch in 1657, passed to the British about 1667, and to the Danes in 1671, who have since held it, except for short occupations by the British. St. Jan was colonized by the Danes in 1684, and their occupancy has since been continuous. St. Croix, or Santa Cruz, was also discovered by Columbus in 1493 or early in 1494, colonized by both Dutch and English in 1625, passed soon to the Spanish, and next to the French in 1651. The Danish ownership dates from 1733. It is isolated in the sea, and not properly of the Virgin Island group; in clear weather, it can be seen from the hills of Porto Rico and from those of St. Thomas and St. Jan.

All three islands are oblong in shape, with the longer axes nearly east and west, the coast lines irregular. The hills of St. Thomas rise to about 1,500 feet; those of St. Jan are somewhat lower (about 1,260 feet), while the highest point on St. Croix (Mt. Eagle) is 1,164 feet. St. Croix is about 21 miles long, 6 miles wide, and has an area of about 84 square miles, being thus about one seventh larger than Staten Island, New York (72½ square miles). St. Thomas is 13 miles long, 4 miles wide, with an area, including its islets, of some 32 square miles; St. Jan is 9 miles long, about 5 miles wide, with an area, in-

cluding its islets, of about 21 square miles. The total area of the three islands, including their contiguous islets, is thus about 138 square miles, or not quite twice that of Staten Island. The areas here used for St. Thomas and St. Jan are approximate, because the total area of the contiguous islets is not definitely recorded.

The harbor of Charlotte Amalia, coveted by commercial and naval interests, is the most striking coastal feature of the islands, indenting the southern coast of St. Thomas. It is something less than a mile in diameter, a little longer than wide, and is nearly enclosed by the hills, its mouth being approximately 900 feet wide. It is as safe an anchorage as any tropical harbor can be, and affords anchorage for as many vessels as would be at all likely to need it at any one time, in water which is up to 37 feet deep. It is not as spacious as Guantanamo Bay on the southeast coast of Cuba, but as a naval base, with the hills fortified, would immediately command the Virgin Passage.

Magen's Bay on the north side of St. Thomas, where a long peninsula juts out into the sea, and Coral Bay at the east and Cruz Bay at the west end of St. Jan, are also valuable harbors, and there are several other small harbors or coves. The so-called harbors at Christiansted and Frederiksted, St. Croix, are open roadsteads.

These islands, like Culebra, Tortola, and Virgin Gorda, are partly plutonic in origin, being partly composed of rocks which have solidified from a molten state. There is no present evidence of volcanic activity, as there is in the Leeward and the Windward Islands farther south, and there are no volcanic peaks. Conglomerate and other stratified rocks, supposed to be Cretaceous, also occur. They are evidently ancient, and show evidences of an enormous amount of erosion since their upheaval; they have not been geologically surveyed.

The soil, except that of some sand beaches and mangrove swamps and salt marshes, has directly resulted from the decay and erosion of the rocks; it is of good agricultural quality and locally deep, but on the steep slopes and hillsides it is meager, having been much washed away since the cutting away of the forests. There are not many sand beaches on St. Thomas or St. Jan, but there is a considerable area of beach on St. Croix. In sheltered coves and reaches with shallow water, the mangrove is forming land, as everywhere in similar situations on tropical coasts.

Along large portions of the coast lines, the rocks come directly to the sea, forming fine cliffs and headlands, often rising from deep water, and much of the coastal scenery is highly picturesque.

I have included records of the plants commonly cultivated either for their products or for ornament and interest, but have made no attempt to include the rarer or unusual garden plants. If the records

by Krebs and Knox are correct, there was a greater variety of plants in gardens at the middle of the last century than at present.

In citing synonyms for the names of plants, I have given the original in cases where the species was first named in a genus other than the one in which it is now included, and I also have indicated the names used by previous authors dealing with plants of the islands, in so far as I have been able to refer them, but no attempt has been made to give complete synonymy.

I gratefully acknowledge aid from Mr. A. S. Hitchcock in the determination of some grasses and from Miss Margaret Slosson and Mr. W. R. Maxon for information regarding some ferns.

## SPERMATOPHYTA

### TYPHACEAE

Typha angustifolia L. [*T. domingensis* Pers.; *T. angustifolia domingensis* Griseb.] Along rivulets and lagoons, St. Thomas; St. Jan; St. Croix.

### PANDANACEAE

Pandanus utilis Bory. [*P. odoratissimus* of Eggers.] Planted for ornament.

### ZANNICHELLIACEAE

Ruppia maritima L. [*R. rostellata* of Eggers.] Shallow, brackish water, St. Thomas; Buck Island; St. Jan; St. Croix.

### CYMODOCEACEAE

Cymodocea manatorum Aschers. Shallow, salt water, St. Croix; St. Thomas; St. Jan.

Halodule Wrightii Aschers. Shallow, salt water, St. Thomas; St. Croix.

### ALISMACEAE

Echinodorus cordifolius (L.) Griseb. [*Alisma cordifolia* L.; *A. rostratum* Nutt.; *Echinodorus rostratus* Engelm.] Wet grounds, St. Thomas; St. Croix.

### ELODEACEAE

Halophila Baillonis Aschers. In salt water, St. Thomas.

Halophila Aschersonii Ostenfeld. In salt water, St. Croix.

### HYDROCHARITACEAE

Thalassia testudinum Konig. In salt water, St. Thomas; St. Jan; St. Croix.

## POACEAE

Saccharum officinarum L. Subspontaneous after cultivation, St. Croix, where it is extensively cultivated for sugar; grown in small patches on St. Thomas and St. Jan.

Andropogon glomeratus (Walt.) B. S. P. Doubtfully recorded from St. Thomas by Hackel.

Andropogon bicornis L. [*Anatherum bicorne* Beauv.] On the high hills of St. Thomas and St. Jan.

Andropogon leucostachyus H.B.K. St. Thomas.

Andropogon juncifolius Desv. St. Croix.

Andropogon ceriferus Hack. St. Thomas.

Andropogon panormitanus Parl. [*A. saccharoides* of Eggers; *A. Wrightii* of Millspaugh.] St. Croix.

Andropogon Schoenanthus L. Cultivated for perfume.

Heteropogon contortus (L.) Beauv. Krumbay, St. Thomas (according to Eggers).

Holcus Sorghum L. [*H. saccharatus* L.; *Sorghum vulgare* Pers.; *Andropogon Sorghum* Brot.] Subspontaneous after cultivation, St. Croix; St. Thomas.

Anthephora hermaphrodita (L.) Kuntze. [*Tripsacum hermaphroditum* L.; *Anthephora elegans* Schreb.; *A. villosa* Spreng.] Waste and cultivated grounds, St. Thomas; St. Croix.

Nazia aliena (Spreng.) Scribn. [*Lappago aliena* Spreng.; *Nazia racemosa aliena* Scribn. & Smith; confused by authors with *Nazia racemosa* (L.) Kuntze = *Tragus racemosus* (L.) Haller.] Sandy fields, thickets and waste grounds, St. Thomas; St. Jan (according to Eggers); St. Croix.

Valota insularis (L.) Chase. [*Andropogon insularis* L.; *Panicum leucophaeum* H.B.K.; *P. insulare* Meyer; *Tricholaena insularis* Griseb.; *Syntherisma insularis* Millsp.] Dry soil, St. Thomas; St. Jan; St. Croix.

Valota Eggersii (Hack.) Hitchc. & Chase. [*Panicum Eggersii* Hack.] St. Thomas. Endemic.

Syntherisma digitata (Sw.) Hitchc. [*Milium digitatum* Sw.; *Digitaria setigera* Roth; *D. horizontalis* Willd.; *Syntherisma setigera* Nash; *P. sanguinale vulgare* of Kuntze in part.] Fields, hills and cultivated grounds, St. Thomas; St. Croix.

Syntherisma sanguinalis (L.) Dulac. [*Panicum sanguinale* L.; *Digitaria marginata* Link.] Fields, hills and cultivated grounds, St. Thomas; St. Jan; St. Croix.

Syntherisma Ischaemum (Schreb.) Nash. [*Panicum Ischaemum* Schreb.] St. Croix (according to Hitchcock & Chase).

The grass recorded by Eggers as *Digitaria filiformis* from Cowell Hill, St. Thomas, has not been further identified.

ERIOCHLOA PUNCTATA (L.) Desv. [*Milium punctatum* L.; *Helopus punctatus* Nees.] Moist grounds, St. Croix; St. Thomas.

ANASTROPHUS COMPRESSUS (Sw.) Schlecht. [*Milium compressum* Sw.; *Paspalum platycaulon* Poir; *P. compressum* Rasp.] Wet grounds, St. Thomas; St. Jan; St. Croix.

PASPALUM GLABRUM Poir. [*P. Helleri* Nash; *Panicum plantagineum* of Millspaugh; ? *P. Richardi* Steud.] Wet grounds, St. Thomas; St. Jan; St. Croix.

PASPALUM PLICATULUM Michx. [*P. undulatum* Poir.; *P. caespitosum* of Eggers, at least in part.] Hillside, Buck Island, St. Thomas; St. Croix (according to Eggers).

PASPALUM PANICULATUM L. [*P. hemisphaericum* Poir.] St. Thomas (according to Schlechtendal).

PASPALUM FIMBRIATUM H.B.K. Waste grounds and roadsides, St. Croix.

PASPALUM ORBICULATUM Poir. [*P. pusillum* Vent.] St. Thomas (Fluegge; according to Grisebach).

PASPALUM CONJUGATUM Berg. Grassy places, St. Thomas; St. Jan; St. Croix.

PASPALUM NOTATUM Fluegge. St. Thomas is the type locality of the species, but the plant has not been found there by recent collectors.

PASPALUM VIRGATUM L. St. Jan; St. Croix (according to West).

PASPALUM SECANS Hitchc. & Chase. Sandy soil, St. Croix.

PASPALUM DISTICHUM L. Wet grounds, St. Thomas; St. Croix.

PASPALUM VAGINATUM Sw. [*P. distichum vaginatum* Sw.] Wet grounds, St. Croix.

PASPALUM SPATHACEUM Desv., recorded as from St. Thomas by Schlechtendal, is a species not understood by modern botanists.

PASPALUM MOLLE Poir., described as from St. Thomas, is a species not understood by modern botanists.

PANICUM GEMINATUM Forsk. [*P. paspaloides* of Eggers and of Millspaugh; *P. brizoides* Lam., not L.; *Paspalum appressum* Lam.] Wet grounds, St. Thomas; St. Jan; St. Croix.

PANICUM BARBINODE Trin. [*P. molle* of Eggers.] Moist grounds, St. Croix.

PANICUM REPTANS L. [*P. grossarium* L.; *P. prostratum* Lam.; *P. prostratum pilosum* Eggers; *P. caespitosum* Sw.] Hillside thickets, St. Thomas; St. Jan; St. Croix.

PANICUM FASCICULATUM Sw. [*P. fuscum* Sw.; *P. fasciculatum fuscum* Griseb.; *P. fasciculatum flavescens* of Kuntze.] Banks, hillsides and thickets, St. Thomas; St. Jan; St. Croix.

PANICUM MILIACEUM L. Waste grounds, St. Croix.

PANICUM ADSPERSUM Trin. Hillside thicket, Bethania, St. Jan.

PANICUM CAYENNENSE Lam. St. Thomas (recorded with doubt by Schlechtendal).

PANICUM DIFFUSUM Sw. Rocky hillsides, St. Thomas; recorded from all three islands by Eggers and from St. Croix by Grisebach.

PANICUM MAXIMUM Jacq. [*P. jumentorum* Pers.; *P. polygamum* Sw.] Dry soil, St. Thomas; St. Jan; St. Croix.

PANICUM LAXUM Sw. Hillsides, St. Thomas.

PANICUM TRICHOIDES Sw. Barracks, St. Thomas (recorded by Eggers as *P. brevifolium* L.).

PANICUM GLUTINOSUM Sw. St. Croix (according to West).

LASIACIS DIVARICATA (L.) Hitchc. [*Panicum divaricatum* L.; *P. divaricatum glabrum* Kuntze.] Thickets and hillsides, St. Thomas; St. Jan; St. Croix.

LASIACIS HARRISII Nash. St. Jan.

LASIACIS SORGHOIDEA (Desvaux) Hitchc. & Chase. [*Panicum sorghoideum* Desvaux; *P. latifolium* of Millspaugh.] Thickets, St. Thomas; St. Croix.

LASIACIS LIGULATA Hitchc. & Chase. [*Panicum divaricatum puberulum* Griseb.] Shaded bank, St. Peter, St. Thomas.

ECHINOCHLOA COLONUM (L.) Link. [*Panicum colonum* L.] Grassy places, waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

OPLISMENUS HIRTELLUS (L.) Beauv. [*Panicum hirtellum* L.; *P. setarium* Lam.; *O. setarius* R. & S.; *Orthopogon setarius* Spreng.] Woodlands, St. Thomas; St. Jan; St. Croix.

CHAETOCHLOA GENICULATA (Lam.) Millsp. & Chase. [*Panicum geniculatum* Lam.; *P. imberbe* Poir.; *Setaria glauca imberbis* Griseb.; *S. glauca* of Eggers; *Chaetochloa glauca* of Millspaugh.] Woodlands, waste and cultivated grounds, St. Thomas; St. Croix; St. Jan.

CHAETOCHLOA SETOSA (Sw.) Scribn. [*Panicum setosum* Sw.; *Setaria setosa* Beauv.; *Panicum caudatum* Lam.; *Setaria setosa caudata* Griseb.; *Setaria macrostachya* of Schlechtendal.] Hillsides, St. Thomas; St. Croix; St. Jan.

CHAETOCHLOA RARIFLORA (Mikan) Hitchc. & Chase. [*Setaria rariflora* Mikan.] Hillsides, St. Thomas; St. Croix.

CENCHRUS ECHINATUS L. [*C. viridis* of Millspaugh; *C. echinatus brevisetus* Scribn.; *C. echinatus tribuloides* of Kuntze.] Fields and hillsides, St. Thomas; St. Jan; St. Croix.

CENCHRUS CAROLINIANUS Walt. St. Thomas (according to Hitchcock & Chase).

CENCHRUS VIRIDIS Spreng. Dry soil, St. Thomas.

STENOTAPHRUM SECUNDATUM (Walt.) Kuntze. [*Ischaemum secun-*

*datum* Walt.; *S. glabrum* Trin.; *S. americanum* Schrank.] Moist grounds, St. Thomas; St. Jan; St. Croix.

OLYRA LATIFOLIA L. Woodlands, St. Thomas; Cinnamon Bay, St. Jan (according to Eggers.)

PHARUS GLABER H.B.K. Woodlands, St. Thomas; St. Jan; St. Croix.

ORYZA SATIVA L. St. Thomas (according to Pilger).

ARISTIDA ADSCENSIONIS L. [*Aristida bromoides* H.B.K.; *A. stricta* Griseb., not Michx.; *A. americana* Pilger, not L.] Thickets and hillsides, St. Thomas; St. Jan; St. Croix.

ARISTIDA COGNATA Trin. & Rupr. [*A. Swartziana* Steud.] Hillsides, St. Thomas; St. Croix.

SPOROBOLUS VIRGINICUS (L.) Kunth. [*Agrostis virginica* L.] Saline soil, St. Thomas; St. Jan; St. Croix.

SPOROBOLUS BERTEROANUS (Trin.) Hitchc. & Chase. [*Vilfa Berteroana* Trin.; *Sporobolus angustus* Buckley.] Wet grounds, St. Jan; St. Croix.

SPOROBOLUS ARGUTUS (Nees) Kunth. [*S. domingensis* of Millspaugh; ? *S. littoralis* of Eggers.] Saline soil, St. Croix.

SPOROBOLUS INDICUS (L.) R. Br. [*Agrostis indica* L.; *Vilfa tenacissima* Kunth.] Dry soil, St. Thomas; St. Jan; St. Croix.

SPOROBOLUS MURALIS (Raddi) Hitchc. & Chase. [*Agrosticula muralis* Raddi; *S. minutiflorus* of Millspaugh.] Waste grounds and roadsides, St. Croix.

CAPRIOLA DACTYLON (L.) Kuntze. [*Panicum Dactylon* L.; *Cynodon Dactylon* Pers.] Dry soil, St. Thomas; St. Jan; St. Croix.

CHLORIS RADIATA (L.) Sw. [*Agrostis radiata* L.] Dry soil, St. Thomas; St. Jan (according to Eggers); St. Croix.

CHLORIS PARAGUAIENSIS Steud. [*C. barbata* Sw.; *C. ciliata* of Eggers.] Waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

CHLORIS SAGRAEANA A. Rich. [*C. eleusinoides* Griseb.] St. Croix.

CHLORIS CILIATA Sw. Dry soil, St. Thomas; St. Croix.

BOUTELOUA AMERICANA (L.) Scribn. [*Aristida americana* L.; *Heterostega juncifolia* Desv.; *B. litigiosa* Lag.] Hillsides and banks, St. Thomas; St. Jan; St. Croix.

GYMNOPOGON FOLIOSUS (Willd.) Nees. [*Chloris foliosa* Willd.] St. Thomas.

ELEUSINE INDICA (L.) Gaertn. [*Cynosurus indicus* L.] Waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

DACTYLOCTENIUM AEGYPTIUM (L.) Richt. [*Cynosurus aegyptius* L.] Waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

LEPTOCHLOA FILIFORMIS (Lam.) Beauv. [*Festuca filiformis* Lam.;

*L. mucronata* (Michx.) Kunth; *L. mucronata multiflora* Eggers.] St. Croix, along ditches (according to Eggers).

LEPTOCHLOA VIRGATA (L.) Beauv. [*Cynosurus virgatus* L.; ? *L. virgata gracilis* Eggers; *Chloris poaeformis* H.B.K.] Moist or wet grounds, St. Thomas; St. Jan; St. Croix.

DIPLACHNE FASCICULARIS (Lam.) Beauv. [*Festuca fascicularis* Lam.; *Leptochloa fascicularis* A. Gray.] In a ditch, St. John's Estate, St. Croix.

PAPPOPHORUM ALOPECUROIDEUM Vahl. [*P. laguroideum* Schrad.] Rocky hillsides, St. Thomas; Buck Island, St. Thomas (according to Eggers).

ERAGROSTIS PILOSA (L.) Beauv. [*Poa pilosa* L.; *E. poaoides* of Grisebach.] Dry soil, St. Thomas; St. Croix.

ERAGROSTIS TEPHROSANTHUS Schultes. Dry soil, St. Thomas; St. Croix.

ERAGROSTIS CILIARIS (L.) Link. [*Poa ciliaris* L.; *E. ciliaris laxa* Kuntze.] Dry soil, St. Thomas; St. Jan; St. Croix.

ERAGROSTIS AMABILIS (L.) Wight & Arn. [*Eragrostis plumosa* Link.] Cultivated grounds, St. Jan.

ERAGROSTIS BARRELIERI Dav. [*E. minor* of Millspaugh; *E. poaoides* of Eggers.] Dry soil, St. Thomas (according to Eggers); St. Croix.

ERAGROSTIS ELLIOTTII S. Wats. Dry soil, St. Thomas.

UNIOLA VIRGATA (Poir.) Griseb. [*Poa virgata* Poir; *U. racemiflora* Trin.] Bolongo, St. Thomas; Little St. James Island, St. Jan.

ARTHROSTYLIDIUM CAPILLIFOLIUM Griseb. Flag Hill, St. Thomas; Battery, St. Jan.

BAMBOS VULGARIS Schrad. Naturalized in wet grounds, St. Thomas; St. Croix.

COIX LACRYMA-JOBI L. Cultivated for ornament.

ZEA MAYS L. Cultivated for food.

## CYPERACEAE

KYLLINGA BREVIFOLIA Rottb. [*K. monocephala* Thunb. of Schlechtendal and of Eggers.] Moist, grassy places, St. Thomas; St. Jan; St. Croix.

KYLLINGA ODORATA Vahl. [*K. triceps* of Eggers; *K. odorata minor* Boeckl.] Moist, shaded banks, St. Thomas; St. Jan.

KYLLINGA PUMILA Michx. Moist grassy places, St. Thomas, collected by Riedlé (according to Clarke).

KYLLINGA PUNGENS Link. Midland, St. Croix.

CYPERUS ODORATUS L. [*C. polystachyus* R. Br.; *Pycraeus odoratus* Urban.] Crown, St. Thomas, at about 500 m. altitude (according to

Eggers). Not found by us on St. Thomas, but collected on Tortola at about the same elevation.

CYPERUS LAEVIGATUS L. [*C. laevigatus albidus* Eggers; *C. mucronatus* Rottb.; *Juncellus laevigatus* Clarke.] Wet grounds, St. Thomas; St. Croix.

CYPERUS SURINAMENSIS Rottb. Wet or moist grounds, St. Thomas.

CYPERUS OCHRACEUS Vahl. Moist grounds, St. Croix.

CYPERUS ELEGANS L. [*C. viscosus* Sw.] Wet saline grounds, St. Thomas; St. Jan; St. Croix.

CYPERUS SPHACELATUS Rottb. Pastures and hillsides, Signal Hill and Crown, St. Thomas.

CYPERUS COMPRESSUS L. Moist ground, Haven Sight, St. Thomas (according to Eggers). Not found by us on St. Thomas, but collected on Virgin Gorda, Vieques and Culebra.

CYPERUS DISTANS L. f. [*Cyperus Eggersii* of Millspaugh.] Pastures and ditches, Signal Hill and St. Peter, St. Thomas; Mt. Eagle, St. Croix.

CYPERUS ESCULENTUS L. [*C. esculentus macrostachyus* Boeckl.] St. Thomas (according to Clarke).

CYPERUS ARTICULATUS L. Wet grounds, St. Thomas; St. Croix.

CYPERUS ROTUNDUS L. [*C. Hydra* Michx.] Waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

CYPERUS CAYENNENSIS (Lam.) Britton. [*Kyllinga cayennensis* Lam.; *Mariscus flavus* Vahl; *Cyperus flavus* Nees; *Cyperus flavomariscus* Griseb.; *Mariscus cayennensis* Urban.] Grassy places, St. Thomas; St. Croix.

CYPERUS GRANULARIS (Desf.) Britton. [*Mariscus gracilis* Vahl; *Kyllinga filiformis capillaris* Griseb.; *C. capillaris* of Millspaugh.] Sandy soil, near the coast, St. Croix.

CYPERUS TENUIS Sw. St. Croix (according to Clarke).

CYPERUS LIGULARIS L. [*Mariscus rufus* H.B.K.; *M. ligularis* Urban.] Moist, especially saline soil, St. Thomas; St. Jan; St. Croix.

CYPERUS CONFERTUS Sw. [*Mariscus confertus* Sw.] Hillsides and thickets, St. Thomas; St. Croix (according to Grisebach).

CYPERUS PURPURASCENS Vahl. Coastal rocks, Water Island, St. Thomas; St. Croix.

CYPERUS BRUNNEUS Sw. [*C. brizaeus* Vahl; *C. Ottonis* Boeckl.; *C. discolor* Boeckl.; *Mariscus brunneus* Clarke.] Coastal sands, St. Thomas; St. Jan; St. Croix.

CYPERUS FERAX L. C. Rich. [*C. pennatus* of Eggers; *C. flexuosus* Vahl; *C. odoratus* of Eggers; *Torulinium ferax* Urban; *C. Michauxianus* of Millspaugh.] Wet grounds, St. Thomas; St. Croix.

CYPERUS VAHLII (Nees) Steud. Moist soil on hills, St. Thomas; St. Jan.

CYPERUS FILIFORMIS Sw. [*Torulinium filiforme* Clarke; *C. unifolius* Boeckl.] Moist soil, St. Thomas; St. Croix.

CYPERUS FERRUGINEUS Poir. [*Pycraeus ferrugineus* Clarke] recorded from St. Thomas by Clarke on the evidence of a specimen in the herbarium of the British Museum, is probably an error in locality.

CYPERUS STRIGOSUS L. Recorded by Schlechtendal as found in a garded on St. Thomas, is probably an error in name.

ELEOCHARIS INTERSTINCTA (Vahl) R. & S. [*Scirpus interstinctus* Vahl.] Marshes, St. Thomas; St. Croix.

ELEOCHARIS MUTATA (Vahl) R. & S. [*Scirpus mutatus* Vahl; *E. cellulosa* of Millspaugh.] Wet grounds, St. Croix; St. Jan (according to Eggers).

ELEOCHARIS FLACCIDA (Spreng.) Urban. [*Scirpus flaccidus* Spreng. *E. ochreata* Nees.] Wet grounds, St. Thomas.

ELEOCHARIS CAPITATA (L.) R. Br. [*Scirpus capitatus* L.] Wet grounds, St. Thomas; St. Jan; St. Croix.

ELEOCHARIS RETROFLEXA (Poir.) Urban. [*Scirpus retroflexus* Poir.; *Eleocharis Chaetaria* R. & S.] Moist grounds, St. Thomas.

ELEOCHARIS MINIMA Kunth. Krumbay, St. Thomas (according to Clarke).

ELEOCHARIS NODULOSA (Roth) Schultes. [*Scirpus nodulosus* Roth.] Adventure, St. Croix (according to Eggers).

SCIRPUS SUBDISTCHUS Boeckl., described as from St. Thomas, has not been identified by subsequent botanists.

SCIRPUS ARTICULATUS (Kunth) Griseb. is recorded as from St. Croix by Kunth, presumably erroneously, it being an Old World species.

FIMBRISTYLIS DIPHYLLA (Retz.) Vahl. [*Scirpus diphyllus* Retz.; *? S. dichotomus* of Schlechtendal; *Scirpus brizoides* Muhl.; *Fimbristylis polymorpha* Boeckl.] Grassy places, St. Thomas; St. Jan; St. Croix.

FIMBRISTYLIS FERRUGINEA (L.) Vahl. [*Scirpus ferrugineus* L.] Moist, saline soil, St. Thomas; St. Jan; St. Croix.

FIMBRISTYLIS SPADICEA (L.) Vahl. [*Scirpus spadiceus* L.] Moist soil near the coast, St. Thomas; St. Croix.

ABILDGAARDIA MONOSTACHYA (L.) Vahl. [*Cyperus monostachyus* L.; *Fimbristylis monostachya* Hassk.] Moist, shaded bank, Rosenberg, St. Jan.

DICHROMENA CILIATA Vahl. [*Rynchospora pura* Griseb.] Pastures and hillsides, Signal Hill and Crown, St. Thomas; Bordeaux, St. Jan.

DICHROMENA RADICANS Schl. & Cham. Shaded banks, St. Thomas.

RYNCHOSPORA BERTERII (Spreng.) Clarke. [*Hypolytrum Berterii* Spreng.; *Rynchospora pusilla* (Sw.) Griseb., not *R. pusilla* Chapm.] Pastures, Signal Hill, St. Thomas (according to Eggers).

RYNCHOSPORA PODOSPERMA C. Wright. St. Thomas; a specimen in the Arnott Herbarium (according to Clarke).

SCLERIA DISTANS Poir. St. Thomas (according to Clarke).

SCLERIA LITHOSPERMA (L.) Sw. [*Scirpus lithospermus* L.; *Scleria filiformis* Sw.] Rocky thickets, St. Thomas; St. Croix.

SCLERIA PTEROTA Presl. [*Scleria pratensis* Nees; *S. communis* of Millspaugh.] Moist woodlands, St. Thomas; St. Jan; St. Croix.

SCLERIA SCINDENS Nees. Forests, Signal Hill, St. Thomas.

## ARECACEAE

COCCOTHRINAX ARGENTEA (Lodd.) Sarg. [*C. sancti-thomae* Beccari; *C. Eggersiana* Beccari; *C. Eggersiana sanctae-crucis* Beccari; *Thrinax argentea* Lodd.; ? *T. parviflora* of Eggers.] Hillsides, Water Island and Flag Hill, St. Thomas; St. Jan; St. Croix.

ACROCOMIA ACULEATA (Jacq.) Lodd. [*Cocos aculeata* Jacq.] Hillside, St. Peter, St. Thomas.

ROYSTONEA REGIA (H.B.K.) O. F. Cook. [? *Areca oleracea* of West; *Oreodoxa regia* H.B.K.; ? *O. oleracea* of Kuntze.] Wooded ravine, Tutu, St. Thomas; St. Croix. Planted for ornament.

COCOS NUCIFERA L. Spontaneous after planting, especially in coastal sands, St. Thomas; St. Jan; St. Croix.

SABAL ——. Planted, Charlotte Amalia, St. Thomas.

BORASSUS FLABELLIFER L. Recorded by West as found on St. Croix. An East Indian palm.

## ARACEAE

ANTHURIUM ACAULE (Jacq.) Schott. [*Pothos acaulis* Jacq.; *Anthurium Huegelii* of Eggers.] On rocks and trees in shaded situations, St. Thomas; St. Jan; St. Croix (according to Eggers).

ANTHURIUM GRANDIFOLIUM (Jacq.) Kunth. [*Pothos grandifolia* Jacq.; *A. macrophyllum* of Eggers.] On rocks in woodlands, St. Thomas; St. Jan.

ANTHURIUM CORDATUM (Willd.) D. Don. [*Pothos cordata* Willd.; ? *P. macrophyllum* of West.] On rocks in forests, St. Jan; St. Croix.

ANTHURIUM SELLOUM C. Koch. On trees and rocks in forests, St. Jan.

PHILODENDRON KREBSII Schott. [*P. hederaceum* of Eggers.] On trees in forests, Crown, St. Thomas.

PHILODENDRON OXYCARDIUM Schott. On trees in forests, St. Thomas.

PHILODENDRON GIGANTEUM Schott. On rocks in dense forests, Signal Hill and Crown, St. Thomas (according to Eggers).

DIEFFENBACHIA SEGUINE (Jacq.) Schott. [*Arum Seguine* Jacq.] Caret Bay, St. Thomas (according to Eggers).

CALADIUM BICOLOR (Ait.) Vent. [*Arum bicolor* Ait.; ? *C. smaragdinum* of Eggers.] St. Thomas (according to Urban). Cultivated on St. Croix.

XANTHOSOMA ATROVIRENS C. Koch. Cultivated and naturalized, St. Thomas; St. Croix (according to Eggers).

XANTHOSOMA SAGITTIFOLIUM (L.) Schott. [*Arum sagittifolium* L.; *Arum maculatum* of Millspaugh.] Naturalized after cultivation, St. Thomas; St. Croix. Cultivated for its roots.

XANTHOSOMA ? HASTATUM Eggers, recorded by Eggers as spontaneous after cultivation on all three islands, has not been identified. *Arum hastatum* Vahl, cited by Eggers as a synonym, is, an unpublished name, printed in West's Flora of St. Croix.

PISTIA STRATIOTES L. [*P. occidentalis* Blume.] Naturalized in gardens, St. Thomas (according to Eggers).

## LEMNACEAE

LEMNA PERPUSILLA Torr. [*L. minor* Eggers; *L. paucicostata* Hegelm.] In still fresh water, St. Croix; St. Jan (according to Eggers).

## BROMELIACEAE

BROMELIA PINGUIN L. Hillsides and thickets; used for hedges, St. Thomas; St. Croix; St. Jan.

WITTMACKIA LINGULATA (L.) Mez. [*Bromelia lingulata* L.; *Chevalliera lingulata* Griseb.] On trees and rocks on hills, St. Thomas; St. Jan.

PITCAIRNIA LATIFOLIA Sol. St. Croix (according to Mez).

PITCAIRNIA ANGUSTIFOLIA (Sw.) Redouté. [*Hepetis angustifolia* Sw.] On rocks, St. Thomas; St. Jan; St. Croix.

CATOPSIS NUTANS (Sw.) Griseb. On trees in forests, high hills of St. Thomas and St. Jan.

TILLANDSIA UTRICULATA L. On trees and rocks, St. Thomas; St. Croix.

TILLANDSIA FASCICULATA L. On trees in woodlands, St. Thomas; St. Jan.

TILLANDSIA RECURVATA L. On trees, St. Thomas; St. Jan; St. Croix.

Eggers records, in his supplementary list, another, undetermined *Tillandsia* from Adrian, St. Jan.

Dendropogon usneoides (L.) Raf. [*Tillandsia usneoides* L.] On trees and shrubs, St. Thomas; St. Jan; St. Croix.

Ananas Ananas (L.) Cook & Collins. [*Bromelia Ananas* L.; *Ananas sativus* Lindl.] Cultivated for its fruit.

## COMMELINACEAE

Commelina longicaulis Jacq. [*C. cayennensis* L. C. Rich.; *C. communis* of West; *C. nudiflora* Clarke, not L.] Moist shaded situations, St. Thomas; St. Jan; St. Croix.

Commelina elegans H.B.K. [*C. virginica* of Millspaugh and of Kuntze.] Moist grounds, St. Thomas; St. Croix.

Callisia repens L. Shaded situations, St. Thomas; St. Jan; St. Croix.

Callisia monandra (Sw.) Schult. [*Tradescantia monandra* Sw.; *Callisia umbellulata* Lam.] Among shaded rocks, Signal Hill, St. Thomas (according to Eggers).

Rhoeo discolor (L'Her.) Hance. [*Tradescantia discolor* L'Her.] Waste rocky places, St. Thomas; St. Jan; St. Croix.

Zebrina pendula Schnitzl. Lawns and cultivated grounds, St. Thomas; St. Croix. Naturalized.

## PONTEDERIACEAE

Piaropus crassipes (Mart.) Raf. [*Pontederia crassipes* Mart.; *Eichhornia crassipes* Solms; *E. azurea* of Millspaugh.] In water, St. Croix.

## LILIACEAE

Aloe vera L. [*Aloe vulgaris* Lam.; *A. perfoliata* of West.] On limestone and in fields, St. Thomas; St. Jan; St. Croix. Naturalized.

**Cordyline guineensis** (Jacq.) Britton. [*Aletris guineensis* Jacq.; *Sanseviera guineensis* Willd.] Hillsides, St. Thomas; St. Croix. Naturalized.

Yucca aloifolia L. [*Y. Draconis* L.] Planted for ornament.

Yucca gloriosa L., is recorded by Eggers as naturalized in gardens and near dwellings on St. Thomas and St. Croix. Planted for ornament.

Allium porrum L. Cultivated for food.

Allium Cepa L. Cultivated for food.

Allium fistulosum L. Cultivated for food.

Allium sativum L. Cultivated for food.

## CONVALLARIACEAE

ASPARAGUS OFFICINALIS L. Planted for food.

## SMILACEAE

SMILAX ILICIFOLIA Kunth. [*S. havenensis* of Eggers.] Hillside thickets, St. Jan (?); St. Croix.

SMILAX CORIACEA Spreng. [*S. subarmata* O. E. Schulz; *S. populnea* of Eggers.] Hillside thickets, St. Thomas; St. Croix.

SMILAX ROTUNDIFOLIA L., cited by O. E. Schulz as from St. Croix, is an error in record or determination.

SMILAX DOMINGENSIS Willd., cited by A. de Candolle from St. Thomas, is an error in locality.

## AMARYLLIDACEAE

ATAMASCO TUBISPATHA (L'Her.) Maza. [*Amaryllis tubispatha* L'Her.; *Zephyranthes tubispatha* Herb.] In fields and near dwellings, St. Thomas; St. Croix; St. Jan (according to Eggers).

ATAMASCO ROSEA (Lindl.) Greene. [*Zephyranthes rosea* Lindl.; ? *Amaryllis Atamasco* of West.] Cultivated for ornament.

CRINUM ERUBESCENS Ait. Along rivulets, St. Croix (according to Eggers); cultivated for ornament.

CRINUM GIGANTEUM Andr. Cultivated for ornament.

CRINUM LONGIFOLIUM Herb. Cultivated for ornament, St. Croix, and seemingly an escape (according to Millspaugh).

HYMENOCALLIS DECLINATA (Jacq.) Roem. [*Hymenocallis expansa* Herb.; *Pancratium caribaeum* of Eggers; *P. declinatum* Jacq.; ? *P. patens* of Schlechtendal; *H. caribaea* of Millspaugh.] Rocky coasts and hillsides, St. Thomas; St. Croix; St. Jan.

HYMENOCALLIS CARIBAEA (L.) Herb. [*Pancratium caribaeum* L.] Planted for ornament.

HIPPEASTRUM PUNICEUM (Lam.) Urban. [*Amaryllis puniceus* Lam.; *A. equestris* Ait.; *Hippeastrum equestre* Herb.] Rocky shores and hillsides, St. Thomas; St. Croix; St. Jan.

AGAVE SISALANA Perrine. Persistent after cultivation, St. Croix. Cultivated for fiber.

AGAVE MISSIONUM Trelease. [*Agave americana* of Eggers in part; *A. sobolifera* and *A. Morrisii* of Eggers.] Hillsides, St. Thomas; St. Jan. Known otherwise on the other Virgin Islands and on Porto Rico.

AGAVE EGGERSIANA Trelease. [*A. americana* of West and of Eggers, in part, and of Millspaugh.] St. Croix. Endemic, but not definitely known in the wild state. Planted for ornament.

FURCRAEA TUBEROSA Ait. f. [*F. cubensis* of Eggers and of Mills-

paugh; *F. hexapetala* of Urban, in part.] Thickets, St. Thomas; St. Croix.

Hypoxis decumbens L. Grassy banks, St. Jan.

Amaryllis Belladonna L. Planted for ornament.

Polianthes tuberosa L. Planted for ornament.

## DIOSCOREACEAE

Dioscorea pilosiuscula Bert. Forests, high hills of St. Thomas; St. Jan.

Dioscorea alata L. Persistent after cultivation, St. Thomas; St. Croix; St. Jan.

Dioscorea sativa L. [*D. altissima* of Eggers, at least in part.] Persistent after cultivation, all islands (according to Eggers). Cultivated for its roots.

Rajania cordata L. [*R. pleironeura* Griseb.; *R. hastata* of Eggers.] Forests, hills of St. Thomas.

## IRIDACEAE

**Galatea bulbosa** (Mill.) Britton. [*Sisyrinchium bulbosum* Mill.; *S. palmifolium* Cav.; *Cipura plicata* Griseb.; *Eleutherine plicata* Herb.] Valleys, St. Croix. Grown in flower gardens.

## MUSACEAE

Musa paradisiaca L. Cultivated for its fruit.

Musa sapientum L. Cultivated for its fruit.

## ZINGIBERACEAE

Alpinia occidentalis Sw. [*Amomum sylvestre* of West; *Renealmia occidentalis* Sweet; *R. sylvestris* of Eggers.] Forests and shaded situations, Golden Rock, St. Croix; Signal Hill, St. Thomas.

Zingiber Zingiber (L.) Karst. [*Amomum Zingiber* L.; *Zingiber officinale* Rosc.] Spontaneous after cultivation. St. Thomas; St. Croix.

Curcuma longa L. Cultivated for tumeric.

Languas speciosa (Wendl.) Small. [*Zerumbet speciosum* Wendl.; *Alpinia nutans* Rosc.] Planted for ornament.

## CANNACEAE

Canna indica L. Moist waste places, St. Thomas; St. Croix (according to Eggers). The plant may have been mistaken for *C. coccinea* Ait.

Canna Lamberti Lindl. Naturalized in gardens, all islands (according to Eggers); escaped in places, St. Croix (according to Millspaugh).

Canna edulis Ker. Cultivated for its tubers.

Canna lutea Mill. Cultivated and escaped in gardens at Bassin, St. Croix (according to Millspaugh).

## MARANTACEAE

Maranta arundinacea L. [*Maranta indica* Tuss. of Millspaugh.] Escaped or spontaneous after cultivation, St. Thomas; St. Croix.

## ORCHIDACEAE

Habenaria monorrhiza (Sw.) Rchb. f. [*Orchis monorrhiza* Sw.; *Habenaria maculosa* of Eggers.] Hillsides, St. Thomas; St. Croix (according to Cogniaux.)

Habenaria alata Hook. Signal Hill, St. Thomas.

Vanilla Eggersii Rolfe. [*V. aphylla* Eggers, not Blume.] Thickets, St. Thomas.

**Beadlea elata** (Sw.) Small. [*Satyrium elatum* Sw.; *Spiranthes elata* L. C. Rich.] In leaf mould and on wet shaded banks on high hills, St. Thomas; St. Jan; St. Croix.

Ibidium tortile (Sw.) House. [*Satyrium tortile* Sw.; *Spiranthes tortilis* L. C. Rich.] Grassy hillsides, St. Thomas.

Stenorrhynchus lanceolatus (Aubl.) Griseb. In clayey soil among rocks, Signal Hill, St. Thomas (according to Eggers.)

Cranichis muscosa Sw. Woods between Crown and Signal Hill, St. Thomas.

Prescottia oligantha (Sw.) Lindl. [*Cranichis oligantha* Sw.; *Prescottia myosurus* Rchb. f.] Grassy fields and banks, hills of St. Thomas; shaded bank, Bordeaux, St. Jan.

Prescottia stachyodes (Sw.) Lindl. [*Cranichis stychyodes* Sw.] Wooded hills, Bordeaux, St. Jan.

Ponthieva glandulosa (Sims) R. Br. [*Neottia glandulosa* Sims.] Wet shaded banks, St. Thomas; St. Jan.

Liparis elata Lindl. Among rocks on high hills, St. Thomas.

Liparis Eggersii Rchb. f. Bonne Résolution, St. Thomas. Perhaps not distinct from the preceding species.

Polystachya minuta (Aubl.) Britton. [*Epidendrum minutum* Aubl.; *Polystachya luteola* Hook.; *Cranichis luteola* Sw.] On rocks, walls and trees, Signal Hill and St. Peter, St. Thomas.

Epidendrum papilionaceum Vahl. [*E. bifidum* Sw.; *E. papilionaceum grandiflorum* Cogn.] On small trees and shrubs, St. Thomas; St. Jan; St. Croix.

EPIDENDRUM CILIARE L. On shaded rocks and trees, St. Thomas; St. Jan; St. Croix.

EPIDENDRUM COCHLEATUM L. On trees, Mt. Eagle and Jacob's Peak, St. Croix (according to Eggers).

EPIDENDRUM PATENS Sw. On rocks, Signal Hill, St. Thomas (acco ding to Eggers).

EPIDENDRUM CARINATUM Vahl, of St. Croix, is a species unknown to modern botanists.

TETRAMICRA ELEGANS (Hamilt.) Cogn. [*Cyrtopodium elegans* Hamilt.; *Epidendrum subaequale* Eggers.] . Rocky hillsides, St. Thomas; St. Jan; St. Croix.

BRASSAVOLA CUCULLATA (L.) R. Br. [*Epidendrum cucullatum* L.] On rocks, St. Thomas.

IONOPSIS UTRICULARIOIDES (Sw.) Lindl. [*Epidendrum utricularioides* Sw.] St. Thomas (according to Cogniaux).

ONCIDIUM LEIBOLDI Rchb. f. Flag Hill, St. Thomas (according to Cogniaux).

ONCIDIUM VARIEGATUM Sw. On shrubs and trees, rarely on rocks, St. Thomas; St. Croix.

ONCIDIUM INTERMEDIUM Bertero. [*O. Lemonianum* Lindl.] Forests and thickets, rare, Picaria Peninsula and Fortuna, St. Thomas (according to Eggers).

## CASUARINACEAE

CASUARINA EQUISETIFOLIA L. Planted; occasionally spontaneous on St. Thomas.

## PIPERACEAE

PIPER AMALAGO L. [*P. medium* Jacq.; *P. Sieberi* C. DC.] Woodlands and forests, St. Thomas; St. Jan; St. Croix.

PIPER DILATATUM L. C. Rich. [*Piper Bredermyeri* of Eggers and of Millspaugh.] Shaded valleys, St. Croix.

PIPER BLATTARUM Spreng. Forests, Crown and Signal Hill, St. Thomas (according to Eggers); known otherwise only from Porto Rico.

PIPER RETICULATUM L. St. Croix (according to West).

PIPER AURITUM Kunth, is recorded by C. de Candolle, with doubt, as collected on St. Thomas by Friedericksthal; the record is probably erroneous.

PIPER TENUIFLORUM Vahl, St. Croix (according to West). A species not understood by modern botanists.

PIPER INCURVUM Sieb., is recorded from St. Croix; the record is questioned by C. de Candolle.

PIPER RETROFRACTUM Vahl. Cultivated on St. Thomas.

POTOMORPHE PELTATA (L.) Miq. [*Piper peltatum* L.; *P. umbellatum* L.] Forests, shaded banks and along rivulets, St. Thomas; St. Croix.

PEPEROMIA GLABELLA (Sw.) A. Dietr. [*Piper glabellum* Sw.] On trees and rocks in forests, St. Thomas; St. Jan.

PEPEROMIA ALATA C. DC. [*P. cubana* of de Candolle, in part.] On trees, St. Croix.

PEPEROMIA PELLUCIDA (L.) H.B.K. [*Piper pellucidum* L.] On walls and in wet shade, St. Thomas; St. Jan; St. Croix; in forests, St. Croix (according to Eggers).

PEPEROMIA SCANDENS R. & P. is recorded by C. de Candolle as found by Friederichsthal on St. Thomas (Prodr. 16[1]: 434, 1869); but in his description of West Indian Piperaceae (Urban Symb. Ant. 3: 229. 1902), St. Thomas is not cited. The earlier record is, presumably, erroneous.

PEPEROMIA GUADALUPENSIS C. DC. [*Piper acuminatum* of West; *P. acuminata* of Eggers, in part.] St. Croix, according to de Candolle, collected by West; on rocks in forests, all islands (according to Eggers).

PEPEROMIA HAMILTONIANA Miquel. [*P. Hamiltoniana emarginula* C. DC.; *P. acuminata* of Millspaugh.] Shaded rocks, St. Croix.

PEPEROMIA MAGNOLIAEFOLIA (Jacq.) A. Dietr. [*Piper magnoliaefolium* Jacq.; ? *Piper obtusifolium* of West; *Peperomia obtusifolia* and *P. obtusifolia clusiaefolia* of Eggers.] In woodlands, St. Thomas; St. Croix.

PEPEROMIA HUMILIS (Vahl) A. Dietr. [*Piper humile* Vahl; *Peperomia Langsdorffii* Miq.; *P. polystachya* of Millspaugh.] Shaded rocks, St. Thomas; St. Jan; St. Croix.

PEPEROMIA MYRTIFOLIA (Vahl) A. Dietr. [*Piper myrtifolium* Vahl.] St. Croix, collected only by Pflug. Endemic.

PEPEROMIA POLYSTACHYA (Ait.) Miq. [*Piper polystachyon* Ait.] St. Croix (according to Hooker); among rocks in forests, all islands (according to Eggers). Perhaps not distinct from *P. humilis*.

PEPEROMIA RUPERTIANA C. DC.(?) Wet, shaded bank, Rosenberg, St. Jan. Determined from a barren specimen, and identification therefore doubtful.

## SALICACEAE

SALIX CHILENSIS Molina. [*S. Humboldtiana* Willd.] In water, near Grove Place, St. Croix.

## ULMACEAE

CELTIS TRINERVIA Lam. Forests and thickets, St. Thomas; St. Jan.

MOMISIA IGUANAEA (Jacq.) Rose & Standley. [*Rhamnus iguanaea* Jacq.; *Celtis aculeata* Sw.; *Celtis aculeata serrata* Eggers.] Thickets, St. Thomas; St. Jan; St. Croix.

TREMA MICRANTHUM (L.) Blume. [*Rhamnus micranthus* L.; *Celtis micrantha* Sw.; *Sponia micrantha* Dcne.] Woodlands, St. Thomas; St. Jan; St. Croix.

## MORACEAE

CHLOROPHORA TINCTORIA (L.) Gaud. [*Morus tinctoria* L.; *Maclura tinctoria* D. Don.] Woodlands, St. Thomas; St. Jan (according to Eggers); St. Croix.

ARTOCARPUS INCISA L. f. Hillsides and valleys, naturalized and planted, St. Thomas; St. Jan; St. Croix.

FICUS URBANIANA Warburg. [*Ficus crassinervia* of Eggers in part, and of Millspaugh.] Woods, St. Croix. Sometimes planted.

FICUS CRASSINERVIA Desf. [*Ficus trigonata* of Eggers.] Forests, St. Thomas; St. Croix.

FICUS LAEVIGATA Vahl. [*Ficus lentiginosa* Vahl; *Ficus populnea* Willd.; *F. thomae* Miq.; *F. sancti-crucis* Miq.; *F. pedunculata* Vahl.] Forests, woodlands and hillsides, St. Thomas; St. Jan; St. Croix.

FICUS CARICA L. Planted for its fruit.

FICUS ELASTICA Roxb. Planted for shade and ornament.

CECROPIA PELTATA L. Forests and hillsides, St. Thomas; St. Jan; St. Croix.

## URTICACEAE

URERA ELATA (Sw.) Griseb. [*Urtica elata* Sw.] Spring Garden, St. Croix, collected by West; Eggers records West's specimen as preserved in the Copenhagen herbarium.

URERA BACCIFERA (L.) Gaud. [*Urtica baccifera* L.] is cited by Eggers as recorded from St. Thomas by Weddell in de Candolle's Prodromus 16[1]: 93, but an examination of pages 93 and 94 of that work does not verify the citation, and the plant is otherwise unknown from these islands.

URTICA ELONGATA Vahl (St. Croix, West) is a species unknown to modern botanists.

FLEURYA AESTUANS (L.) Gaud. [*Urtica aestuans* L.] On rocks, walls and in forests, St. Thomas; St. Jan; St. Croix.

PILEA MICROPHYLLA (L.) Liebm. [*Parietaria microphylla* L.; *Adicea microphylla* Kuntze; *P. microphylla trianthemoides* and *succulenta* of Eggers; *Adicea microphylla trianthemoides* and *succulenta* of Millspaugh.] Rocky situations, St. Thomas; St. Jan; St. Croix.

PILEA TENERRIMA Miquel. Shaded banks, St. Jan.

PILEA RICHARDI Urban. St. Thomas, collected by L. C. Richard, the specimen preserved in the Copenhagen herbarium (according to Urban). Endemic.

PILEA INAEQUALIS (Juss.) Wedd. [*Urtica inaequalis* Juss.; *Adicea inaequalis* Kuntze.] On rocks in forests, Signal Hill and Crown, St. Thomas.

PILEA SANCTAE-CRUCIS Liebm. [*Adicea sanctae-crucis* Kuntze; *Pilea semidentata* of Eggers; *Pilea grandis* of Eggers.] Forests, St. Thomas; St. Jan; St. Croix.

PILEA NUMMULARIAEFOLIA (Sw.) Wedd. [*Urtica nummulariaefolia* Sw.; *Adicea nummulariaefolia* Kuntze.] Shaded situations, St. Thomas; St. Croix.

PILEA GRANDIFOLIA (L.) Blume. [*Pilea grandis* Wedd.] Recorded by de Candolle (Prodr. 16[1]: 143) as from Jamaica and St. Thomas, is confined to Jamaica, where there is a parish of St. Thomas.

ROUSSELIA HUMILIS (Sw.) Urban. [*Urtica humilis* Sw.; *U. lappulacea* Sw.; *Rousselia lappulacea* Gaud.] Shaded situations, St. Thomas.

## OLACACEAE

SCHOEPFIA SCHREBERI Gmelin. [*Codonium arborescens* Vahl; *S. arborescens* R. & S.] Woodlands, St. Thomas; St. Croix.

## LORANTHACEAE

DENDROPEMON CARIBAEUS Krug & Urban. [*Loranthus emarginatus* of Eggers; *Phthirusa caribaea* Engler.] On trees, St. Thomas; St. Jan; St. Croix.

PHORADENDRON CHRYSOCARPUM Krug & Urban. [*Phoradendron flavens* of Eggers; *P. martinicense* of Millspaugh.] On trees, St. Thomas; St. Croix.

PHORADENDRON TRINERVIUM (Lam.) Griseb. is recorded by Trelease as represented in the Ventenat Herbarium by a specimen from St. Thomas; it is otherwise unknown from the islands.

PHORADENDRON RACEMOSUM (Aubl.) Krug & Urban. [*P. pennineruium* O. Kuntze] is recorded by O. Kuntze as from St. Thomas, apparently erroneously; the specimen was probably from Porto Rico.

## ARISTOLOCHIACEAE

ARISTOLOCHIA ODORATISSIMA L. Hillside thickets, St. Jan.

ARISTOLOCHIA TRILOBATA L. Thickets, St. Thomas; St. Jan; St. Croix (according to West).

ARISTOLOCHIA ANGUICIDA L. Thickets, St. Croix.

ARISTOLOCHIA RINGENS Vahl. Cultivated on St. Croix (according to West).

## POLYGONACEAE

COCCOLOBIS KRUGII Lindau. Rocky Hills, Little St. James Island, St. Jan.

COCCOLOBIS PYRIFOLIA Desf. [*C. Kunthiana* Meissn.; *C. pyrifolia Jacquini* of Eggers.] St. Thomas (according to Lindau).

COCCOLOBIS OBTUSIFOLIA Jacq. [*C. microstachys* Willd.; *C. microstachya ovalifolia* Meissn.; *C. punctata microstachya* of Eggers; *C. punctata parvifolia* of Millspaugh.] Thickets, St. Thomas; St. Jan; St. Croix.

COCCOLOBIS KLOTZSCHIANA Meissn. St. Thomas and St. Croix (according to Lindau). Endemic. Perhaps not distinct from the preceding species.

COCCOLOBIS DIVERSIFOLIA Jacq. [*C. barbadensis* Jacq.; *C. punctata* of Eggers; *C. coronata* of Millspaugh.] Woods and thickets, St. Thomas; St. Jan; St. Croix.

COCCOLOBIS LAURIFOLIA Jacq. [*C. leoganensis* of Eggers.] Thickets, St. Croix.

COCCOLOBIS RUGOSA Desf. St. Thomas (according to de Candolle, a specimen being preserved in the Delessert Herbarium); not known to be on St. Thomas at the present time but may have been there before the forests were cut away; known otherwise only from Porto Rico.

COCCOLOBIS UVIFERA (L.) Jacq. [*Polygonum Uvifera* L.; *C. leoganensis* Jacq.; *Uvifera leoganensis* Kuntze.] Coastal thickets and locally on hills, St. Thomas; St. Jan; St. Croix.

COCCOLOBIS VENOSA L. [*C. excoriata* L.; *C. nivea* Jacq.] Woods and hillsides, St. Thomas; St. Croix.

ANTIGONUM CINERASCENS M. & G. [*A. cordatum* of Eggers and of Millspaugh.] Roadsides, St. Thomas; cultivated for ornament, St. Thomas and St. Croix.

FAGOPYRUM FAGOPYRUM (L.) Karst. [*Polygonum Fagopyrum* L.] Planted for food.

RUMEX VESICARIUS L. Recorded by Eggers as cultivated.

MUHLENBECKIA PLATYCLADA (F. Muell.) Lindau. Planted for interest.

## CHENOPODIACEAE

CHENOPODIUM MURALE L. Walls and waste grounds, St. Thomas; St. Croix.

CHENOPODIUM AMBROSIOIDES L. [? *C. cuneifolium* Vahl.] Walls and waste grounds, St. Thomas; St. Jan; St. Croix.

ATRIPLEX PENTANDRA (Jacq.) Standley. [*Axyris pentandra* Jacq.; *Atriplex cristata* H. & B.; *Obione cristata* Moq.] Coastal sands, St. Thomas; St. Jan; St. Croix.

SALICORNIA PERENNIS Mill. [*S. ambigua* Michx.] Salt marshes, St. Croix.

BETA VULGARIS L. Cultivated for food.

## AMARANTHACEAE

CELOSIA NITIDA Vahl. [? *C. paniculata* of Schlechtendal.] Woods and thickets, St. Thomas; St. Jan; St. Croix.

CELOSIA ARGENTEA L. [*C. margaritacea* L.] Waste and cultivated grounds, St. Thomas; St. Croix.

CELOSIA CRISTATA L. Planted for ornament.

CHAMISSOA ALTISSIMA (Jacq.) H.B.K. [*Achyranthes altissima* Jacq.; *Kokera paniculata* Kuntze.] Forests and thickets, St. Thomas; St. Croix.

AMARANTHUS DUBIUS Mart. [*A. tristis* Willd., not L.; *A. paniculatus* of Eggers and of Millspaugh.] Waste grounds, St. Thomas; St. Jan; St. Croix.

AMARANTHUS SPINOSUS L. Waste and cultivated grounds, St. Thomas; St. Croix.

AMARANTHUS CRASSIPES Schl. [*Scleropus amarantoides* Schrad.] Dry soil, waste and cultivated grounds, St. Thomas; St. Croix.

AMARANTHUS CAUDATUS L. St. Croix (according to West).

AMARANTHUS POLYGONOIDES L. [*Amblyogyne polygonoides* Raf.] Sandy soil, roadsides and waste grounds, St. Thomas; St. Croix.

AMARANTHUS GRACILIS Desf. [*Chenopodium caudatum* Jacq.; ? *Amaranthus oleraceus* of West; *Euxolus caudatus* Moq.; *E. oleraceus* of Eggers.] Waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

AMARANTHUS GANGETICUS L. [*A. incomptus* Willd.; *A. tricolor* L.] Planted for ornament.

CENTROSTACHYS INDICA (L.) Standley. [*Achyranthes aspera indica* L.; *Achyranthes aspera obtusifolia* Griseb.; *A. aspera simplex* Millsp.] Waste and cultivated grounds, St. Thomas; St. Croix.

CENTROSTACHYS ASPERA (L.) Standley. [*Achyranthes aspera* L.; *A. argentea* Lam.] is recorded from the islands by Eggers, but I have seen no specimens nor find any other record; the plant occurs, however, on Tortola.

ACHYRANTHES POLYGONOIDES (L.) Lam. [*Gomphrena polygonoides* L.; *Alternanthera polygonoides* R. Br.; *Alternanthera paronychioides* St. Hil.] Waste grounds, St. Thomas.

ACHYRANTHES REPENS L. [*Alternanthera Achyrantha* R. Br.; *A. paronychioides* of Millspaugh.] Rocky waste places, St. Thomas; St. Croix.

ACHYRANTHES FICOIDEA (L.) Standley. [*Gomphrena ficoidea* L.;

*Illecebrum ficoideum* L.; *Alternanthera ficoidea* R. Br.] Moist places and on shores, St. Thomas.

Achyranthes portoricensis (Kuntze) Standley. [*Alternanthera portoricensis* Kuntze.] Rocky hills, Little St. James Island, St. Jan.

Gomphrena globosa L. Subspontaneous after cultivation, St. Thomas; St. Croix.

Iresine angustifolia Euphr. [*I. elatior* L. C. Rich.] Thickets, and banks, St. Thomas; St. Croix.

Philoxerus vermiculatus (L.) R. Br. [*Illecebrum vermiculatum* L.; *Lithophila vermiculata* Uline; *Iresine vermicularis* Miq.] Saline soil along the coasts, St. Thomas; St. Croix.

Lithophila muscoides Sw. Rocks on the shore, Judith's Fancy, St. Croix.

## NYCTAGINACEAE

Mirabilis jalapa L. [*M. dichotoma* L.] Waste grounds, St. Thomas; St. Croix.

Boerhaavea erecta L. Waste and cultivated ground, St. Croix.

Boerhaavea coccinea Mill. [*B. paniculata* L. C. Rich.; *B. diffusa* Sw.; *B. decumbens* Vahl; *B. hirsuta* Willd.; *B. diffusa paniculata* Kuntze; *B. repens* of Millspaugh.] Dry soil, St. Thomas; St. Croix; St. Jan.

Commicarpus scandens (L.) Standley. [*Boerhaavea scandens* L.] Rocky hillsides, St. Thomas.

Pisonia aculeata L. Hillsides, woods and thickets, St. Thomas; St. Croix.

Pisonia subcordata Sw. [*P. nigricans* of West.] Thickets and woods, St. Thomas; St. Croix.

Torrubia fragrans (Dum.-Cours.) Standley. [*Pisonia fragrans* Dum.-Cours.; *Pisonia inermis* of Eggers, of Kuntze and of Millspaugh; ? *P. coccinea* of West.] Forests and thickets, St. Thomas; St. Croix.

Bougainvillea spectabilis Willd. Cultivated for ornament.

Eggersia buxifolia Hook. f. [*Neea buxifolia* Heimerl.] Dry hillsides, St. Thomas; St. Jan.

## BATIDACEAE

Batis maritima L. Shores of salt water lagoons, St. Thomas; St. Croix.

## PHYTOLACCACEAE

Rivina humilis L. [*R. laevis* L.; *Tithonia humilis* Kuntze.] Dry, shaded situations, St. Thomas; St. Jan; St. Croix.

Trichostigma octandrum (L.) H. Walt. [*Rivina octandra* L.; *Villamilla octandra* Hook. f.; *Rivina scandens* Mill.] Woods and thickets, St. Thomas; St. Jan; St. Croix.

PETIVERIA ALLIACEA L. Dry, shaded situations, St. Thomas; St. Jan; St. Croix.

MICROTEA DEBILIS Sw. Waste grounds, St. Thomas; St. Croix.

## AIZOACEAE

MOLLUGO VERTICILLATA L. Dry soil, Buck Island, St. Thomas;

MOLLUGO NUDICAULIS L. Rocky soil and banks, St. Thomas. St. Croix.

SESUVIUM PORTULACASTRUM L. [*Halimus portulacastrum* Kuntze.] Saline soil, St. Thomas; St. Jan; St. Croix.

TRIANTHEMA PORTULACASTRUM L. [*T. monogynum* L.] Waste and rocky places. St. Thomas; St. Croix.

CYPSELEA HUMIFUSA Turp. Around a small fresh-water lagoon, Water Island, St. Thomas (according to Eggers).

## PORTULACACEAE

TALINUM TRIANGULARE (Jacq.) Willd. [*Portulaca triangularis* Jacq.] Rocky soil, St. Thomas; St. Croix.

TALINUM PANICULATUM (Jacq.) Gaertn. [*Portulaca paniculata* Jacq.; *P. patens* Jacq.; *Talinum patens* Willd.] Rocky soil, St. Thomas; St. Jan; St. Croix.

PORTULACA OLERACEA L. [*P. oleracea macrantha* and (?) *micrantha* Eggers.] Sunny situations, St. Thomas; St. Jan; St. Croix.

PORTULACA PILOSA L. Cultivated and waste grounds, St. Thomas; St. Croix.

PORTULACA HALIMOIDES L. Sunny situations, St. Thomas; St. Jan; St. Croix.

PORTULACA QUADRIFIDA L. Waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

PORTULACA BRASILIENSIS West, of St. Croix, is not described. The plant was probably one of the preceding species.

## BASELLACEAE

BOUSSINGAULTIA LEPTOSTACHYS Moq. [*B. baselloides* of Eggers.] Naturalized in gardens and cultivated, St. Thomas; St. Croix.

BASELLA RUBRA L. Cultivated on St. Croix.

## ALSINACEAE

DRYMARIA CORDATA (L.) Willd. [*Holosteum cordatum* L.; *D. cordata diandra* Eggers.] Shaded moist places, St. Thomas; St. Croix.

## NYMPHAEACEAE

CASTALIA AMPLA (DC.) Salisb. [*Nymphaea ampla* DC.; *N. ampla parvifolia* Eggers.] In rivulets and ponds, St. Croix.

## MENISPERMACEAE

CISSAMPELOS PARIERA L. [*C. microcarpa* DC.] Woods and thickets, St. Thomas; St. Croix; St. Jan.

HYPERBAENA LAURIFOLIA (Poir.) Urban. [*Cissampelos laurifolius* Poir.; *Cocculus laurifolius* of Eggers.] Woodlands, St. Thomas.

HYPERBAENA DOMINGENSIS (DC.) Benth. [*Cocculus domingensis* DC.] Forest, near St. Peter, St. Thomas (according to Eggers). The species is not accredited to St. Thomas by Urban (Symb. Ant. 1: 306). Eggers's record probably refers to *H. laurifolia*.

## ANNONACEAE

OXANDRA LAURIFOLIA (Sw.) A. Rich. [*Uvaria laurifolia* Sw.; *U. excelsa* Vahl.] St. Croix (according to West).

GUATTERIA CARIBAEA Urban. [*G. Ouregou* Griseb., not Dunal.] St. Thomas (according to Grisebach).

ANNONA MURICATA L. Woods and thickets, St. Thomas; St. Jan; St. Croix.

ANNONA PALUSTRIS L. [*A. glabra* L.; *A. laurifolia* Dunal.] Borders of marshes and coastal thickets, St. Thomas; St. Croix.

ANNONA SQUAMOSA L. [*Annona cinerea* Dunal.] Woods, hillsides and thickets, St. Thomas; St. Jan; St. Croix.

ANNONA RETICULATA L. Woods and hillsides, St. Thomas; St. Jan; St. Croix.

ANNONA MONTANA Macf. Fredericksted, St. Croix.

## LAURACEAE

HUFELANDIA PENDULA (Sw.) Nees. [*Laurus pendula* Sw.; *H. thomae* Nees.] St. Thomas (DC. Prodr. $15^1$: 65); recorded from St. Thomas as collected by Riedlé (Mez, Jahrb. Bot. Gart. Berlin 5: 21).

ACRODICLIDIUM SALICIFOLIUM (Sw.) Griseb. Forests, St. Thomas; St. Jan; St. Croix.

PERSEA PERSEA (L.) Cockerell. [*Laurus Persea* L.; *Persea americana* Mill.; *P. gratissima* Gaertn. f.] Spontaneous after planting, St. Thomas; St. Croix.

PHOEBE CUBENSIS Nees. [*P. antillana cubensis* Meissn.; *P. elongata* of Eggers.] St. Croix (West, according to DC. Prodr. $15^1$: 31, and also recorded by Mez).

Ocotea leucoxylon (Sw.) Mez. [*Laurus leucoxylon* Sw.; *Oreodaphne leucoxylon* Nees.] Forest, Signal Hill, St. Thomas.

Ocotea floribunda (Sw.) Mez. [*Laurus floribunda* Sw.] Wooded hillside, Bordeaux, St. Jan.

Nectandra antillana Meissn. Forests, St. Thomas.

Nectandra membranacea (Sw.) Griseb. [*Laurus membranacea* Sw.] Dense forests, Signal Hill, St. Thomas; Will's Bay, St. Croix (according to Eggers).

Nectandra coriacea (Sw.) Griseb. [*Laurus coriacea* Sw.] Forests, St. Thomas; St. Jan; St. Croix.

Laurus indica West, of St. Croix, is unknown to modern botanists.

Laurus longifolia Vahl, collected on St. Croix by West, is not further determined.

Cinnamomum zeylanicum Blume is recorded by Eggers as naturalized in a few places in shaded valleys on St. Croix.

## CASSYTHACEAE

Cassytha americana Nees. Coastal thickets, St. Thomas; St. Croix.

## PAPAVERACEAE

Argemone mexicana L. Waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

## CAPPARIDACEAE

Cleome spinosa Jacq. [*C. pungens* Willd.] Waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

Cleome gynandra L. [*C. pentaphylla* L.; *Gynandropsis pentaphylla* DC.] Waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

Cleome viscosa L. [*Polanisea icosandra* of Millspaugh.] Waste and cultivated grounds, St. Thomas; St. Croix.

Capparis cynophallophora L. [*C. jamaicensis* Jacq.; *C. torulosa* of West; *C. jamaicensis marginata* and *siliquosa* Eggers; ? *C. linearis* of West.] Thickets and hillsides, St. Thomas; St. Jan; St. Croix.

Capparis indica (L.) Fawc. & Rend. [*Breynia indica* L.; *Capparis Breynia* Jacq.; *C. amygdalina* Lam.; *C. Grisebachii* of Millspaugh.] Thickets, woods and hillsides, St. Thomas; St. Jan; St. Croix.

Capparis baducca L. [*Capparis frondosa* Jacq.] Forests and hillsides, St. Thomas; St. Croix; St. Jan (according to Eggers).

Capparis flexuosa L. [*Capparis cynophallophora* of Eggers and

of Millspaugh; *C. saligna* of West; *C. cynophallophora saligna* Eggers.] Woods, thickets and hillsides, St. Thomas; St. Jan; St. Croix.

CAPPARIS COCCOLOBIFOLIA Mart. [*C. cynophallophora latifolia* Griseb.] Thickets and hillsides, St. Thomas; St. Jan; St. Croix.

CAPPARIS PORTORICENSIS Urban. Hillside thicket between Bethania and Rosenberg, St. Jan.

CAPPARIS VERRUCOSA Jacq. St. Thomas (according to Grisebach); Virgin Islands (according to Eggers).

MORISONIA AMERICANA L. Wooded hillsides, St. Thomas; St. Jan; St. Croix (according to Eggers).

## BRASSICACEAE

LEPIDIUM VIRGINICUM L. [*L. apetalum* of Millspaugh.] Waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

LEPIDIUM SATIVUM L. Cultivated for condiment.

CAKILE LANCEOLATA (Willd.) O. E. Schulz. [*C. aequalis* L'Her.] Coastal sands and rocks, St. Thomas; St. Jan; St. Croix.

SINAPIS ARVENSIS L. Naturalized near Anguilla, St. Croix (according to Eggers).

BRASSICA INTEGRIFOLIA (West) O. E. Schulz. [*Sinapis integrifolia* West; *S. brassicata* Griseb., not L.; *S. juncea* of Millspaugh.] Waste and cultivated grounds, St. Thomas; St. Croix; St. Jan.

BRASSICA OLERACEA L. Cultivated for food.

BRASSICA CAMPESTRIS L. [*B. Rapa* L.] Cultivated for food.

SISYMBRIUM NASTURTIUM L. [*Nasturtium officinale* R. Br.] In rivulets, St. Thomas; St. Croix.

RAPHANUS RAPHANISTRUM L. Recorded by West.

RAPHANUS SATIVUS L. Cultivated for food.

KONIGA MARITIMA (L.) R. Br. [*Clypeola maritima* L.] Cultivated for ornament.

## MORINGACEAE

MORINGA MORINGA (L.) Millsp. [*Guilandina Moringa* L.; *Hyperanthera Moringa* Vahl; *Moringa pterygosperma* Gaertn.] Roadsides and hillsides, St. Thomas; St. Jan; St. Croix.

## CRASSULACEAE

BRYOPHYLLUM PINNATUM (Lam.) Kurz. [*Cotyledon pinnata* Lam.; *B. calycinum* Salisb.] Dry soil, St. Thomas; St. Jan; St. Croix.

## ROSACEAE

A number of different kinds of roses are grown for ornament.

## AMYGDALACEAE

CHRYSOBALANUS ICACO L. Woods, hillsides and thickets, St. Thomas; St. Jan; St. Croix.

## MIMOSACEAE

INGA LAURINA (Sw.) Willd. [*Mimosa laurina* Sw.; *M. laurifolia* of West.] Woodlands and forests, St. Thomas; St. Jan; St. Croix.

PITHECOLOBIUM UNGUIS-CATI (L.) Mart. [*Mimosa unguis-cati* L.; *Inga Unguis-cati* Willd.; *P. Unguis-cati forfex* Griseb.] Thickets, hillsides and pastures, St. Thomas; St. Jan; St. Croix.

ENTEROLOBIUM SAMAN (Jacq.) Prain. [*Mimosa Saman* Jacq.; *Calliandra Saman* Griseb.; *Pithecolobium Saman* Benth.] Roadsides and near settlements, St. Thomas; St. Croix.

ALBIZZIA LEBBECK (L.) Benth. [*Mimosa Lebbeck* L.; *M. speciosa* Jacq.; *Acacia Lebbeck* Willd.] Fields and hillsides, St. Thomas; St. Croix.

**Anneslia portoricensis** (Jacq.) Britton. [*Mimosa portoricensis* Jacq.; *Calliandra portoricensis* Benth.] Forests, King's Hill, St. Jan.

**Anneslia haematostoma** (Bert.) Britton. [*Acacia haematomma* Bert.; *Calliandra haemotomma* Benth.] Flag Hill, St. Thomas.

**Anneslia purpurea** (L.) Britton. [*Calliandra purpurea* Benth.; *Mimosa purpurea* L.; *Inga purpurea* Willd.] Cultivated on St. Croix (according to West).

ACACIA NUDIFLORA Willd. Hillsides and woods, St. Thomas; St. Jan.

ACACIA RIPARIA H.B.K. [*A. sarmentosa* Griseb., not Desv.; *Mimosa paniculata* of West; *A. Westiana* DC.] Hillsides and thickets, St. Thomas; St. Jan; St. Croix (according to West).

ACACIA CATECHU Willd. [*Mimosa catechu* L. f.] Naturalized in shaded valleys, St. Croix.

ACACIA MACRACANTHA H. & B. [*Mimosa lutea* Houst.; *Acacia lutea* Hitchc., not Leavenw.; *A. macracantha glabrens* Eggers.] Hillsides and thickets, St. Thomas; St. Jan; St. Croix.

ACACIA TORTUOSA (L.) Willd. [*Mimosa tortuosa* L.] Hillsides, St. Thomas; St. Croix.

ACACIA ARABICA Willd., is planted for ornament, and is recorded by Eggers as naturalized near dwellings on St. Thomas and St. Croix.

VACHELLIA FARNESIANA (L.) W. & A. [*Mimosa Farnesiana* L.; *Acacia Farnesiana* Willd.] Hillsides and thickets, St. Thomas; St. Jan; St. Croix.

LEUCAENA GLAUCA (L.) Benth. [*Mimosa glauca* L.; *Acacia frondosa* Willd.] Fields and hillsides, St. Thomas; St. Jan; St. Croix.

MIMOSA PUDICA L. Fields and hillsides, St. Thomas; St. Croix.

MIMOSA CERATONIA L. [? *M. sensitiva* of West.] Hills and thickets, St. Thomas; St. Jan; ? St. Croix (according to West).

MIMOSA PIGRA L. [*M. asperata* L.] St. Thomas (according to Grisebach), who indicates that he saw a specimen from that island, but the plant has not been found there by recent collectors.

ACUAN VIRGATUM (L.) Medic. [*Mimosa virgata* L.; *Desmanthus virgatus* Willd.; *D. strictus* Bertol.; *D. virgatus strictus* Griseb.; *A. virgatus albiflorus* Kuntze.] Fields and hillsides, St. Thomas; St. Croix.

ACUAN DEPRESSUM (H. & B.) Kuntze. [*Desmanthus depressus* H. & B.] Hillsides, St. Thomas; St. Jan.

NEPTUNIA PUBESCENS Benth. Buck Island, St. Thomas (according to Eggers).

ADENANTHERA PAVONINA L. Naturalized, St. Thomas; St. Jan and St. Croix (according to Eggers); not seen by us on any of the islands, except as a planted tree.

## CAESALPINACEAE

HYMENAEA COURBARIL L. Woods and hillsides, St. Thomas; St. Jan; St. Croix.

TAMARINDUS INDICA L. In various situations, St. Thomas; St. Jan; St. Croix. Planted for its fruit and for shade.

BAUHINIA TOMENTOSA L. Spontaneous after cultivation, waste grounds, St. Thomas; St. Croix.

BAUHINIA MONANDRA Kurz. [*B. Kappleri* Sagot; *B. Krugii* Urban.] Spontaneous after planting, St. Thomas; St. Croix.

BAUHINIA UNGULA Jacq., recorded by Grisebach as found on St. Thomas, is probably an error in record or determination.

CASSIA FISTULA L. Naturalized in shaded valleys, St. Croix (according to Eggers). Planted for shade and for its fruit.

CASSIA GRANDIS L. Naturalized on St. Thomas and St. Croix.

CASSIA QUINQUANGULATA L. C. Rich. [*C. bacillaris* of Eggers, of Kuntze and of Millspaugh.] Woods and thickets, St. Thomas.

CASSIA BICAPSULARIS L. Waste grounds and hillsides, St. Thomas; St. Jan; St. Croix.

CASSIA SIAMEA Lam. [*C. florida* Vahl.] Naturalized near towns, St. Thomas (according to Eggers). Planted for shade and ornament.

CASSIA OCCIDENTALIS L. [*C. planisiliqua* L.] Waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

CASSIA TORA L. [*C. obtusifolia* L.] Waste and cultivated grounds, St. Thomas; St. Croix.

Cassia polyphylla Jacq. [*C. biflora angustisiliqua* of Eggers.] Hillsides, St. Thomas; St. Croix.

Cassia obovata Collad. Naturalized on St. Thomas (according to Eggers).

Cassia hirsuta L. Sugar Estate, St. Thomas (according to Eggers).

Cassia alata L. Waste grounds, St. Thomas; St. Jan; St. Croix.

Cassia augustifolia Vahl. Planted on St. Croix (according to West).

Cassia triflora Vahl, collected on St. Croix by Rohr, is "a doubtful species" according to Eggers; it is not the same as *Cassia triflora* Jacquin, a prior name.

Cassia grandis L. [*C. mollis* Vahl.] Planted for shade.

Chamaecrista grammica (Spreng.) Pollard. [*Cassia grammica* Spreng.] Rocky soil, Little St. James Island, St. Jan.

Chamaecrista Swartzii (Wickstr.) Britton. [*Cassia Swartzii* Wickstr.; *C. glandulosa* of West; *Cassia glandulosa stricta* and *ramosa* of Eggers; *Chamaecrista glandulosa* and *C. glandulosa ramosa* of Millspaugh; *Chamaecrista complexa* Pollard; *Cassia Chamaecrista pubicaulis* Kuntze.] Fields and hillsides, St. Thomas; St. Jan; St. Croix.

Chamaecrista Chamaecrista (L.) Britton. [*Cassia Chamaecrista* L.; *Cassia nictitans* of Eggers and of Millspaugh; *C. diffusa* DC.] Dry, grassy situations, St. Thomas; St. Jan; St. Croix.

Parkinsonia aculeata L. Coastal thickets, St. Thomas; St. Jan; St. Croix.

Haematoxylon campechianum L. [*Sabinea florida* of Millspaugh.] Coastal thickets and hillsides, St. Thomas; St. Jan; St. Croix.

Delonix regia (Bojer) Raf. [*Poinciana regia* Bojer.] Spontaneous after planting, St. Thomas; St. Croix.

Guilandina Crista (L.) Small. [*Caesalpinia Crista* L.; *Guilandina Bonducella* L.] Coastal sands, St. Thomas; St. Jan; St. Croix.

Guilandina divergens (Urban) Britton. [*Caesalpina divergens* Urban; *Guilandina Bonduc* of Schlechtendal and of Eggers.] Coastal thickets, St. Thomas; St. Jan; St. Croix.

Guilandina melanosperma Eggers. [*Caesalpinia melanosperma* Urban.] Coastal thickets, St. Croix.

Caesalpinia coriaria Willd. [*Poinciana coriaria* Jacq.; *Lebidibia coriaria* Schl.] Hillsides, St. Thomas. Planted on St. Croix.

Caesalpinia Gilliesii Wall. [*Poinciana Gilliesii* Hook.] Planted for ornament.

Caesalpinia punctata Willd. Planted on St. Thomas.

CAESALPINIA SAPPAN L. Recorded by Krebs as planted on St. Thomas.

CAESALPINIA ELATA Sw. Attributed by Eggers to St. Croix, presumably erroneously.

POINCIANA PULCHERRIMA L. [*Caesalpinia pulcherrima* Sw.] Spontaneous after cultivation, St. Thomas; St. Croix.

## KRAMERIACEAE

KRAMERIA IXINA L. [*K. Ishami* Millsp.] Dry rocky soil, Bovoni and Water Island, St. Thomas.

## FABACEAE

MYROSPERMUM FRUTESCENS Jacq. Naturalized near dwellings, St. Croix (according to Eggers).

SOPHORA TOMENTOSA L. Coastal sands, St. Thomas; St. Croix.

CROTALARIA RETUSA L. Waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

CROTALARIA JUNCEA L. Field at Bassin, St. Croix; recorded by West as cultivated prior to 1793.

CROTALARIA VERRUCOSA L. Waste and cultivated grounds, St. Thomas; St. Croix; St. Jan.

CROTALARIA INCANA L. Waste and cultivated grounds, St. Thomas; St. Croix.

CROTALARIA LOTIFOLIA L. Thickets and hillsides, St. Thomas; St. Jan; St. Croix.

CROTALARIA LABURNIFOLIA L. Cultivated on St. Croix (according to West).

INDIGOFERA SUFFRUTICOSA L. [*I. Anil* L.] Thickets and hillsides, St. Thomas; St. Jan; St. Croix.

INDIGOFERA GUATEMALENSIS Moç. & Sessé. St. Thomas.

INDIGOFERA TINCTORIA L. Thickets, St. Thomas; St. Jan; St. Croix (according to Eggers, who notes its former cultivation).

MEDICAGO SATIVA L. Planted on St. Croix.

PAROSELA DOMINGENSIS (DC.) Millsp. [*Dalea domingensis* DC.; *D. phymatodes* of Eggers.] Dry soil, St. Jan, collected only by Eggers.

CRACCA CINEREA (L.) Morong. [*Galega cinerea* L.; *G. littoralis* L.; *Tephrosia cinerea* Pers.; *Cracca villosa cinerea* Kuntze; *Tephrosia cinerea littoralis* of Eggers.] Dry sandy soil, St. Thomas; St. Jan; St. Croix.

CRACCA PURPUREA L. [*Galega purpurea* L.] Cultivated on St. Croix (according to West).

SABINEA FLORIDA (Vahl) DC. [*Robinia florida* Vahl.] Hillsides and thickets, St. Thomas; St. Jan.

Benthamantha caribaea (Jacq.) Kuntze. [*Galega caribaea* Jacq.; *Cracca caribaea* Benth; *Brittonamra caribaea* Kuntze.] Thickets and hillsides, St. Thomas; St. Croix.

Coursetia arborea Griseb., recorded by Grisebach from St. Jean, is erroneously quoted by Eggers as from St. Jan. There is a place called St. Jean in French Guiana.

Sesban sericea (Willd.) DC. [*Coronilla sericea* Willd.] Thickets, Flag Hill, St. Thomas.

**Sesban Sesban** (L.) Britton. [*Aeschynomene Sesban* L.] Planted on St. Croix.

Agati grandiflora (L.) Desv. [*Aeschynomene grandiflora* L.; *Sesbania grandiflora* Pers.] Roadsides and near dwellings, naturalized St. Thomas; St. Jan; St. Croix.

Pictetia aculeata (Vahl) Urban. [*Robinia aculeata* Vahl; *R. squamata* Vahl; *Aeschynomene aristata* Jacq.; *Pictetia squamata* DC.; *P. aristata* DC.] Woods, hillsides and thickets, St. Thomas; St. Jan; St. Croix.

Aeschynomene americana L. [*Ae. americana depila* Millsp.] Grassy places, St. Thomas; St. Jan; St. Croix.

Stylosanthes hamata (L.) Taubert. [*Hedysarum hamatum* L.; *Stylosanthes procumbens* Sw.] Dry soil, St. Thomas; St. Croix; St. Jan.

Stylosanthes viscosa Sw., recorded by West from St. Croix. Eggers thought perhaps a mistake for the preceding species, which is probable.

Arachis hypogaea L. Subspontaneous after cultivation, St. Thomas; St. Croix. Hardly persistent.

Zornia diphylla (L.) Pers. [*Hedysarum diphyllum* L.; *Z. reticulata* Smith.] Pastures, high hills of St. Thomas; St. Croix (according to de Candolle).

Codariocalyx gyrans (L. f.) Hassk. [*Hedysarum gyrans* L. f.; *Desmodium gyrans* DC.] Planted for interest.

Meibomia triflora (L.) Kuntze. [*Hedysarum triflorum* L.; *Desmodium triflorum* DC.; *Meibomia triflora pilosa* Kuntze.] Fields and moist grassy places, St. Thomas; St. Jan; St. Croix.

Meibomia supina (Sw.) Britton. [*Hedysarum supinum* Sw.; *H. incanum* Sw.; *Desmodium supinum* DC.; *D. incanum* DC.] Fields, hillsides, woods and thickets, St. Thomas; St. Jan; St. Croix.

Meibomia axillaris (Sw.) Kuntze. [*Hedysarum axillare* Sw.; *Desmodium axillare* DC.] Shaded banks and ravines, St. Croix.

Meibomia mollis (Vahl) Kuntze. [*Hedysarum molle* Vahl; *Desmodium molle* DC.] Grassy places, St. Thomas; St. Croix.

Meibomia spiralis (Sw.) Kuntze. [*Hedysarum spirale* Sw.; *Des-*

*modium spirale* DC.] Hillsides and banks, St. Thomas; St. Jan; St. Croix.

Meibomia tortuosa (Sw.) Kuntze. [*Hedysarum tortuosum* Sw.; *Desmodium tortuosum* DC.] Banks, hillsides and thickets, St. Thomas; St. Croix.

Meibomia scorpiurus (Sw.) Kuntze. [*Hedysarum scorpiurus* Sw.; *Desmodium scorpiurus* Desv.] Grassy places, St. Thomas (according to Grisebach); St. Croix (according to Eggers).

Lourea vespertilionis (L.) Desv. [*Hedysarum vespertilionis* L.] Naturalized in gardens, St. Thomas; St. Croix (according to Eggers). Planted for ornament.

Alysicarpus nummularifolius (L.) DC. [*Hedysarum nummularifolium* L.; *H. vaginale* L.; *Alysicarpus vaginalis* DC.] Waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

**Ecastophyllum Ecastophyllum** (L.) Britton. [*Hedysarum Ecastophyllum* L.; *Pterocarpus Ecastophyllum* of West; *Ecastophyllum Brownei* Pers.; *Dalbergia Ecastophyllum* Taubert.] Coastal thickets, St. Thomas; St. Jan; St. Croix.

Drepanocarpus lunatus (L. f.) Meyer. [*Pterocarpus lunatus* L. f.] Coastal thickets, St. Thomas; St. Croix (according to West and to Eggers).

Ichthyomethia Piscipula (L.) Hitchc. [*Erythrina Piscipula* L.; *Piscidia Erythrina* L.; *P. Piscipula* Sargent.] Thickets and woodlands, St. Thomas; St. Jan; St. Croix.

Andira jamaicensis (W. Wright) Urban. [*Geoffraea jamaicensis* (*inermis*) W. Wright; *G. inermis* Sw.; *Andira inermis* H.B.K.; *Vouacapoua americana* of Millspaugh.] Woods and along rivulets, St. Thomas; St. Jan; St. Croix.

Abrus Abrus (L.) W. F. Wight. [*Glycine Abrus* L.; *Abrus praecatorius* L.] Thickets and hedges, St. Thomas; St. Jan; St. Croix.

Clitoria ternatea L. [*Ternatea vulgaris* H.B.K.] Thickets and hedges, St. Thomas; St. Jan; St. Croix.

Bradburya virginiana (L.) Kuntze. [*Clitoria virginiana* L.; *Centrosema virginianum* Benth.; *C. virginianum angustifolium* Griseb.] Banks, fields and hillsides, St. Thomas; St. Jan; St. Croix.

Bradburya Plumieri (Turp.) Kuntze. [*Clitoria Plumieri* Turp.; *Centrosema Plumieri* Benth.] Sugar Estate, St. Thomas.

Teramnus labialis Spreng. [*T. uncinatus albiflorus* Eggers.] Thickets, St. Thomas; St. Jan; St. Croix.

Erythrina corallodendron L. Hillsides, St. Thomas; St. Croix. Planted for shade and ornament.

Erythrina horrida Eggers. Hillside, Flag Hill, St. Thomas. Recorded from all three islands by Eggers.

MUCUNA PRURIENS (L.) DC. [*Dolichos pruriens* L.] Shaded valleys and rocky banks, St. Thomas; St. Croix.

GALACTIA DUBIA DC. [*G. tenuiflora* of Eggers, partly; *G. regularis* of Millspaugh; *G. dubia Ehrenbergii* Urban; *G. filiformis minor* + *villosa* f. *albida* Kuntze.] Hillsides and thickets, St. Thomas; St. Jan; St. Croix.

GALACTIA STRIATA (Jacq.) Urban. [*Glycine striata* Jacq.; *G. striata tomentosa* Urban; *G. filiformis* of Eggers; *G. tenuiflora* of Millspaugh.] Thickets, St. Thomas; St. Jan; St. Croix.

GALACTIA EGGERSII Urban. [*G. tenuiflora* of Eggers; *G. pendula* of Knox.] Hillside, Flag Hill, St. Thomas; Bordeaux, St. Jan. Endemic.

CANAVALI RUSIOSPERMA Urban. [*C. parviflora* of Eggers.] Forest, Signal Hill, St. Thomas.

CANAVALI ENSIFORMIS (L.) DC. [*Dolichos ensiformis* L.; *C. gladiata ensiformis* of Eggers.] Naturalized in provision grounds, Signal Hill, St. Thomas (according to Eggers). Cultivated for its seeds.

CANAVALI LINEATA (Thunb.) DC. [*Dolichos lineatus* Thunb.; *D. rotundifolius* Vahl; *Dolichos obtusifolius* Lam.; *Canavalia obtusifolia* DC.] Coastal sands, St. Thomas; St. Jan; St. Croix.

CAJAN CAJAN (L.) Millsp. [*Cytisus Cajan* L.; *Cajanus flavus* DC.; *Cajanus indicus* Spreng.] Spontaneous after cultivation, St. Thomas; St. Jan; St. Croix.

DOLICHOLUS RETICULATUS (Sw.) Millsp. [*Glycine reticulata* Sw.; *Rhynchosia reticulata* DC.; *R. reticulata latifolia* Kuntze.] Roadsides and thickets, St. Thomas; St. Jan; St. Croix.

DOLICHOLUS PHASEOLOIDES (Sw.) Kuntze. [*Glycine phaseoloides* Sw.; *Rhynchosia phaseoloides* DC.] Forest, Signal Hill, St. Thomas (according to Eggers).

DOLICHOLUS MINIMUS (L.) Medic. [*Dolichos minimus* L.; *Rhynchosia minima* DC.; *R. punctata* DC.; *R. minima lutea* Eggers; *D. minimus luteus* Millsp.] Banks, hillsides and thickets and in cultivated ground, St. Thomas; St. Jan; St. Croix.

PHASEOLUS LUNATUS L. Thickets, spontaneous after cultivation, St. Thomas; St. Jan; St. Croix.

PHASEOLUS VULGARIS L. Spontaneous after cultivation, St. Thomas; St. Jan; St. Croix.

PHASEOLUS LATHYROIDES L. [*P. semierectus* L.] Banks, fields and hillsides, St. Thomas; St. Jan; St. Croix.

PHASEOLUS ALATUS L., recorded from St. Croix by West, is not further determined.

VIGNA REPENS (L.) Kuntze. [*Dolichos repens* L.; ? *D. luteus* of

West; *Dolichos luteolus* Jacq.; *Vigna luteola* Benth.; *Bradburya pubescens* of Millspaugh, St. Thomas.] Moist thickets, St. Thomas; St. Jan; St. Croix.

Vigna unguiculata (L.) Walp. [*Dolichos unguiculatus* L.; *D. Catjang* L.; *Vigna Catjang* Walp.] Edge of a cornfield near Doily Hill, St. Croix; St. Thomas (according to Schlechtendal).

Pachyrrhizus erosus (L.) Urban. [*Dolichos erosus* L.; *Pachyrrhizus angulatus* L. C. Rich.] Hillside thickets, St. Thomas.

Dolichos Lablab L. [*Lablab vulgaris* Savi; *Dolichos benghalensis* Jacq.; *Dolichos Lablab abliflorus* (DC.) Millsp.] Thickets and spontaneous after cultivation, St. Thomas; St. Jan; St. Croix.

Dolichos sphaerospermus (L.) DC. [*Phaseolus sphaerospermus* L.] Cultivated for its seeds.

Dolichos sesquipedalis L. Cultivated for its seeds.

Brownea coccinea Jacq. Planted on St. Croix (according to West).

Pisum sativum L. Cultivated for its seeds.

## OXALIDACEAE

Ionoxalis intermedia (A. Rich.) Small. [*Oxalis intermedia* A. Rich.; *O. latifolia* of Millspaugh.] Cultivated grounds, St. Croix.

Ionoxalis Martiana (Zucc.) Small. [*Oxalis Martiana* Zucc.] Shaded banks, St. Thomas; cultivated grounds, St. Croix.

Xanthoxalis corniculata (L.) Small. [*Oxalis corniculata* L.; *O. corniculata microphylla* of Eggers.] Dry soil, St. Thomas; St. Jan; St. Croix.

## GERANIACEAE

*Pelargoniums* are cultivated for ornament.

## BALSAMINACEAE

Impatiens Balsamina L. [*Balsamina hortensis* Desp.] Grown in flower gardens.

## ERYTHROXYLACEAE

Erythroxylon brevipes DC. [*E. ovatum* of Eggers, of Millspaugh, and of Kuntze; *E. areolatum* of West.] Hillsides and thickets, St. Thomas; St. Croix.

Erythroxylon areolatum L. is doubtfully attributed to St. Thomas by O. E. Schulz.

## ZYGOPHYLLACEAE

Guaiacum officinale L. Woods and thickets, St. Thomas; formerly on St. Croix and St. Jan. Nearly exterminated. Planted on St. Thomas.

TRIBULUS CISTOIDES L. [*T. terrester cistoides* Oliver.] Dry soil, St. Croix.

KALLSTROEMIA MAXIMA (L.) T. & G. [*Tribulus maximus* L.] Waste and cultivated grounds, St. Thomas; St. Croix; St. Jan.

## RUTACEAE

ZANTHOXYLUM PUNCTATUM Vahl. [*Fagara trifoliata* Sw.; *Tobinia punctata* Griseb.] Thickets and banks, St. Croix.

ZANTHOXYLUM THOMASIANUM Krug & Urban. [? *Tobinia spinosa* of Eggers.] Forest, Flag Hill, St. Thomas; St. Jan. Endemic.

ZANTHOXYLUM SPINIFEX (Jacq.) DC. [*Fagara spinifex* Jacq.; *F. tragodes* of West; *Zanthoxylum microphyllum* Desv.] Thickets, St. Croix.

ZANTHOXYLUM MONOPHYLLUM (Lam.) P. Wilson. [*Fagara monophylla* Lam.; *Zanthoxylum simplicifolium* Vahl; *Z. Ochroxylum* DC.] Hillsides, woods and thickets, St. Thomas; St. Jan; St. Croix.

ZANTHOXYLUM MARTINICENSE (Lam.) DC. [*Fagara martinicensis* Lam.; *Zanthoxylum Clava-Herculis* of Eggers.] Woods and hillsides, St. Thomas; St. Jan; St. Croix.

ZANTHOXYLUM FLAVUM Vahl. [*Fagara flava* Krug & Urban.] Bordeaux Hills, St. Jan, nearly extinct (according to Eggers). Not found by us on St. Jan in 1913.

PILOCARPUS RACEMOSUS Vahl. Forest, King's Hill, St. Jan.

AMYRIS ELEMIFERA L. [*A. maritima* Jacq.; *A. sylvatica* of Eggers.] Woods and thickets, St. Thomas; St. Jan; St. Croix (according to Eggers).

CHALCAS EXOTICA (L.) Millsp. [*Murraya exotica* L.] Spontaneous after cultivation, St. Thomas; St. Croix.

TRIPHASIA TRIFOLIA (Burm. f.) P. Wilson. [*Limonia trifolia* Burm. f.; *T. trifoliata* (L.) DC.] Spontaneous after cultivation, naturalized in thickets, St. Thomas; St. Jan; St. Croix.

CITRUS MEDICA L. Recorded by Eggers as naturalized in gardens.

CITRUS LIMA Lunan. [*C. medica Limonum* of Eggers; *C. Limetta* Wight.] Woodlands and thickets, naturalized, St. Thomas; St. Jan; St. Croix.

CITRUS AURANTIUM L. Occasionally spontaneous after planting, St. Thomas; St. Croix.

CITRUS VULGARIS Risso. [*C. Bigaradia* Loisel.; *C. Aurantium bigaradia* Griseb.] Occasionally spontaneous after planting, St. Thomas; St. Croix.

CITRUS DECUMANA L. Planted for its fruit.

CITRUS BUXIFOLIA Poir. Planted for its fruit (according to Eggers).

CLAUSENA WAMPI Blanco. [*Cookia punctata* Sonn.] Planted for shade.

## SURIANACEAE

SURIANA MARITIMA L. Coastal sands, St. Thomas; St. Jan; St. Croix.

## SIMAROUBACEAE

QUASSIA AMARA L. Naturalized in and about gardens, St. Thomas; St. Croix. Planted for shade.

CASTELARIA NICHOLSONI (Hook.) Small. [*Castela Nicholsoni* Hook.; *C. erecta* of Eggers and of Millspaugh.] Thickets, St. Croix.

AESCHRION ANTILLANA (Eggers) Small. [*Rhus antillana* Eggers; *Quassia excelsa* of West; *Picrasma antillana* Urban; *Picraena excelsa* of Eggers and of Millspaugh.] Forests, St. Thomas; St. Jan; St. Croix.

## BURSERACEAE

ELAPHRIUM SIMARUBA (L.) Rose. [*Pistacia Simaruba* L.; *Bursera gummifera* L.; *Bursera Simaruba* Sargent.] Woods and hills, St. Thomas; St. Jan; St. Croix.

TETRAGASTRIS BALSAMIFERA (Sw.) Kuntze. [*Hedwigia balsamifera* Sw.; ? *Icica altissima* of West.] St. Croix (according to West).

## MELIACEAE

SWIETENIA MAHAGONI Jacq. Hillsides and valleys, St. Thomas; St. Croix. Often planted; perhaps not native.

MELIA AZEDARACH L. Roadsides; occasional in woods, St. Thomas; St. Jan; St. Croix.

TRICHILIA HIRTA L. [*T. spondioides* Jacq.] Woods, thickets and hillsides, St. Thomas; St. Jan; St. Croix.

TRICHILIA WAWRANA ANTILLANA C. DC., described as from St. Croix from a specimen in the Copenhagen herbarium, is otherwise unknown.

GUAREA TRICHILIOIDES L., was recorded by West from St. Croix, but the record was questioned by Eggers. It is abundant in Porto Rico.

## MALPIGHIACEAE

HIRAEA FAGINEA (Sw.) Ndz. [*H. faginea glandulifera* Ndz.], recorded by Niedenzu from St. Thomas, is probably an error in locality.

BANISTERIA PURPUREA L. [*Heteropteris purpurea* H.B.K.; *H. parvifolia* DC.] Thickets and hillsides, St. Thomas; St. Jan; St. Croix.

Banisteria laurifolia L. [*Heteropteris laurifolia* A. Juss.; *B. laurifolia antillana* Ndz., *B. lancifolia* of West.] St. Croix (according to Niedenzu).

Stigmaphyllon lingulatum (Poir.) Small. [*Triopteris lingulata* Poir.; *Banisteria periplocifolia* Desf.; *Stigmaphyllon periplocifolium* A. Juss.; *S. Sagraeanum* of Millspaugh.] Thickets and hillsides, St. Thomas; St. Jan; St. Croix.

Stigmaphyllon cordifolium Ndz. St. Thomas (according to Niedenzu).

Stigmaphyllon ciliatum (Lam.) A. Juss., recorded by Niedenzu from St. Thomas, as collected by Finlay, was really from Trinidad.

Stigmaphyllon tomentosum (Desf.) Ndz. [*Banisteria tomentosa* Desf.] Royiers, St. Jan (according to Niedenzu).

Spachea littoralis A. Juss., recorded by A. Jussieu as collected by Finlay on St. Thomas, was from Trinidad.

Thryallis glauca (Cav.) Kuntze. [*Galphimia glauca* Cav.; *G. gracilis* Bartl.] Roadsides and about dwellings, naturalized, St. Thomas; St. Croix.

Tetrapteris inaequalis Cav. St. Croix (according to Niedenzu).

Malpighia fucata Ker. [*M. fucata elliptica* Ndz.] St. Croix (according to Eggers).

Malpighia glabra L. [*M. glabra antillana* Urban & Ndz.] Thickets, St. Thomas; St. Croix (according to Eggers and to Niedenzu).

Malpighia punicifolia L. [*M. punicifolia vulgaris* and *lancifolia* Ndz.; *M. glabra* of Millspaugh.] Hillsides and thickets, St. Thomas; St. Croix.

Malpighia linearis Jacq. [*M. angustifolia* L.; *M. angustifolia oblongata* Ndz.; ? *M. urens lanceolata* Eggers.] Hillside thickets, Water Island, St. Thomas; St. Jan.

Malpighia biflora Poir. [*M. oxycocca Grisebachiana* Ndz.] St. Croix (according to Niedenzu).

Malpighia pallens Small. [*M. urens* of Millspaugh? and of Eggers.] Thickets along sandy beaches, St. Croix. Endemic.

Malpighia infestissima (A. Juss.) Rich. [*M. urens* of West; *M. urens infestissima* A. Juss.; *M. Cnide* of Eggers.] Hillside thickets, Water Island, St. Thomas; St. Jan. Also on Vieques and Culebra. Endemic. St. Thomas is the type locality.

Bunchosia glandulosa (Cav.) DC. [*Malpighia glandulosa* Cav.; *M. Swartziana* of Eggers.] Thickets, St. Thomas; St. Jan; St. Croix.

Byrsonima spicata (Cav.) DC. [*B. coriacea* of Millspaugh.] Woods and thickets, St. Thomas; St. Jan; St. Croix.

Byrsonima cuneata (Turcz.) P. Wilson. [*B. lucida* DC.] St. Thomas (according to de Candolle, and cited also by Niedenzu).

Byrsonima martinicensis Krug & Urban. St. Croix (according to Small).

## POLYGALACEAE

Polygala angustifolia H.B.K. Thickets, southern side of St. Thomas.

Securidaca Brownei Griseb. [*S. scandens* West.] Naturalized around Christiansted, St. Croix, and on St. Thomas (according to Eggers).

Securidaca erecta L. Dry soil, St. Croix; St. Thomas (according to de Candolle).

## EUPHORBIACEAE

Savia sessiliflora (Sw.) Willd. [*Croton sessiliflorum* Sw.] Thickets and hillsides, St. Thomas; St. Jan; St. Croix.

**Asterandra grandifolia** (L.) Britton. [*Phyllanthus grandifolius* L.] St. Thomas (according to Urban).

Phyllanthus Niruri L. Waste and cultivated grounds, St. Thomas; St. Croix.

Phyllanthus acuminatus Vahl is accredited to St. Thomas by Mueller (DC. Prodr. $15^2$: 381) who records a specimen in the Candollean herbarium, but the shrub is not known to inhabit St. Thomas now.

Cicca disticha L. [*Phyllanthus distichus* Muell. Arg.] Spontaneous after planting, St. Thomas; St. Jan; St. Croix.

Margaritaria nobilis L. f. [*Phyllanthus nobilis* Muell. Arg.; *Cicca antillana* A. Juss.; *P. nobilis antillanus* Muell. Arg.] Forests, St. Thomas; St. Jan; St. Croix (according to Eggers).

Securinega Acidothamnus (Griseb.) Muell. Arg. [?*Adelia Acidoton* of West; *Flueggea Acidothamnus* Griseb.] Thickets, St. Thomas; Little St. James Island, St. Jan; eastern St. Croix (according to Eggers).

Drypetes glauca Vahl. St. Croix (according to Eggers).

Croton astroites Dryand. [*C. phlomoides* Pers.] Thickets, St. Thomas; St. Jan; St. Croix.

Croton betulinus Vahl. Thickets, St. Thomas; St. Jan; St. Croix.

Croton flavens L. [*C. balsamifer* Jacq.; *C. flavens rigidus* Muell. Arg.; *Oxydestes flavens* Kuntze.] Thickets, St. Thomas; St. Jan; St. Croix.

Croton discolor Willd. Rocky thickets, St. Thomas; St. Croix.

Croton lobatus L. [*Oxydectes lobata* Kuntze.] Waste and cultivated grounds, St. Thomas; St. Croix; St. Jan.

Croton humilis L. Hillside thickets, St. Thomas.

Croton glandulosus L. St. Croix (according to Urban).

CROTON OVALIFOLIUS Vahl. [*Oxydectes ovalifolia* Kuntze.] Hillsides, St. Thomas; St. Jan; St. Croix.

CROTON HASTATUS West, of St. Croix (hyponym) is not identified.

An arboreus Croton, not found in flower, occurred on Flag Hill, St. Thomas, according to Eggers.

DITAXIS FASCICULATA Vahl. [*Argyrothamnia fasciculata* Muell. Arg.] Thickets, St. Thomas; St. Jan; St. Croix.

ARGYTHAMNIA CANDICANS Sw. Thickets and hillsides, St. Thomas; St. Jan; St. Croix.

RICINELLA RICINELLA (L.) Britton. [*Adelia Ricinella* L.; *R. pedunculosa* Muell. Arg.] Hillsides and thickets, St. Thomas; St. Jan; St. Croix.

ACALYPHA PORTORICENSIS Muell. Arg. Rocky slopes, St. Croix.

ACALYPHA CHAMAEDRIFOLIA (Lam.) Muell. Arg. [*Croton chamaedrifolius* Lam.; *Acalypha reptans* Sw.; *A. corchorifolia* Willd.; *A. chamaedrifolia genuina* and *brevipes* of Eggers.] Rocky soil, St. Thomas; St. Croix.

ACALYPHA POLYSTACHYA Jacq. St. Thomas (according to Eggers). The record is probably an error in determination.

TRAGIA VOLUBILIS L. Thickets, banks and hillsides, St. Thomas; St. Jan; St. Croix.

DALECHAMPIA SCANDENS L. Thickets, St. Thomas; St. Jan; St. Croix.

RICINUS COMMUNIS L. Waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

ALEURITES MOLUCCANA (L.) Willd. [*Jatropha moluccana* L.] Roadsides and near dwellings, St. Thomas; St. Croix.

JATROPHA CURCAS L. Hillsides and near dwellings, St. Thomas; St. Jan; St. Croix.

JATROPHA GOSSYPIFOLIA L. [*Adenoropium gossypifolium* Pohl; *J. gossypifolia staphisagriaefolia* and *elegans* of Eggers.] In dry soil, fields and hillsides, St. Thomas; St. Jan; St. Croix.

JATROPHA MULTIFIDA L. Roadsides and planted in gardens, St. Thomas; St. Croix.

JATROPHA PANDURAEFOLIA Andr. Planted for ornament.

MANIHOT MANIHOT (L.) Cockerell. [*Jatropha Manihot* L.] Spontaneous or persistent after cultivation, St. Thomas; St. Jan; St. Croix.

SAPIUM LAUROCERASUS Desf. [*Excoecaria Laurocerasus* Muell. Arg.; ? *E. Laurocerasus laurifolia* of Eggers.] A high tree in forests, Cinnamon Bay, St. Jan, not seen flowering (according to Eggers). Otherwise known only from Porto Rico.

HIPPOMANE MANCINELLA L. Coastal woods, St. Thomas; St. Croix.

GYMNANTHES LUCIDA Sw. [*Sebastiana lucida* Muell. Arg.] Woods and thickets, St. Thomas; St. Jan; St. Croix.

HURA CREPITANS L. Woods, roadsides and near dwellings, St. Thomas; St. Jan; St. Croix.

CHAMAESYCE VAHLII (Willd.) P. Wilson. [*Euphorbia Vahlii* Willd.] Rocky hills, Little St. James Island, St. Jan.

CHAMAESYCE BUXIFOLIA (Lam.) Small. [*Euphorbia buxifolia* Lam.; *E. glabrata* Sw.] Coastal sands, St. Thomas; St. Jan; St. Croix.

CHAMAESYCE ARTICULATA (Aubl.) Britton. [*Euphorbia articulata* Aubl.; *E. linearis* Retz.; *E. linearis heterophylla* Kuntze.] Coastal rocks, St. Thomas; St. Jan; St. Croix (according to Retzius and reported by Eggers).

CHAMAESYCE HIRTA (L.) Millsp. [*Euphorbia hirta* L.; *E. pilulifera* L.; *E. pilulifera procumbens* Boiss.] Roadsides, banks and cultivated grounds, St. Thomas; St. Jan; St. Croix.

CHAMAESYCE HYPERICIFOLIA (L.) Millsp. [*Euphorbia hypericifolia* L.; *E. hypericifolia hyssopifolia* of Eggers.] Fields, banks and cultivated grounds, St. Thomas; St. Jan; St. Croix.

CHAMAESYCE SERPENS (H.B.K.) Small. [*Euphorbia serpens* H.B.K.] Dry soil, St. Thomas.

CHAMAESYCE PROSTRATA (Ait.) Small. [*Euphorbia prostrata* Ait.; ? *E. Chamaesyce* of West.] Waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

CHAMAESYCE BRASILIENSIS (Lam.) Small. [*Euphorbia brasiliensis* Lam.] Grassy places near Charlotte Amalia, St. Thomas, determined by Millspaugh.

EUPHORBIA THYMIFOLIA Burm. is recorded by Eggers from all the islands, but has not been found on any of them by other collectors, and his determination of the species is therefore doubted.

AKLEMA PETIOLARIS (Sims.) Millsp. [*Euphorbia petiolaris* Sims.; ? *E. cotinifolia* of West and of Schlechtendal.] Hillsides and thickets, St. Thomas; St. Jan; doubtfully recorded from St. Croix.

POINSETTIA HETEROPHYLLA (L.) Kl. & Garcke. [*Euphorbia heterophylla* L.; *E. heterophylla linifolia* Kuntze.] Dry rocky situations, St. Thomas.

POINSETTIA CYATHOPHORA (Murr.) S. Brown. [*Euphorbia cyathophora* Murr.; *E. heterophylla cyathophora* Griseb.] Waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

POINSETTIA OERSTEDIANA Kl. & Garcke. [*Euphorbia geniculata* of Eggers; *Euphorbia Oerstediana* Boiss.] Grassy places, St. Thomas; St. Croix.

POINSETTIA PULCHERRIMA (Willd.) Graham. [*Euphorbia pulcherrima* Willd.] Planted for ornament.

EUPHORBIA NERIIFOLIA L. Planted for ornament.

EUPHORBIA SPLENDENS Bojer. Planted for ornament.

EUPHORBIA ANTIQUORUM L. Cultivated (according to Eggers).

PEDILANTHUS TITHYMALOIDES (L.) Poit. [*Euphorbia tithymaloides* L.] Persistent after cultivation, St. Thomas. Grown in flower gardens.

PEDILANTHUS PADIFOLIUS (L.) Poit. [*Euphorbia tithymaloides padifolia* L.] Thickets in dry stony ground, St. Croix.

PEDILANTHUS ANGUSTIFOLIUS Poit. Thickets and hillsides, St. Thomas; St. Jan.

CODIAEUM VARIEGATUM Blume. Planted for ornament.

## BUXACEAE

TRICERA VAHLII (Baill.) Britton. [*Buxus Vahlii* Baill.; *Tricera laevigata sanctae-crucis* Eggers.] On limestone, Stony Ground, St. Croix. Known otherwise only on Porto Rico.

MANGIFERA INDICA L. Spontaneous after planting, St. Thomas; St. Jan; St. Croix.

ANACARDIUM OCCIDENTALE L. Woods, hillsides and along roads, St. Thomas; St. Jan; St. Croix.

SPONDIAS PURPUREA L. Spontaneous after planting, St. Thomas; St. Jan; St. Croix.

SPONDIAS MOMBIN L. [*Spondias lutea* L.] Woods, hills and roadsides, St. Thomas; St. Jan; St. Croix.

SPONDIAS DULCIS Forst. f. Cultivated on St. Croix.

COMOCLADIA DODONAEA (L.) Urban. [*Ilex Dodonaea* L.; *Comocladia ilicifolia* Sw.] Rocky coastal thickets, St. Thomas; St. Jan; St. Croix.

## CELASTRACEAE

MAYTENUS ELLIPTICA (Lam.) Krug & Urban. [*Senacia elliptica* Lam.; *Rhamnus laevigatus* Vahl; *Ceanothus laevigatus* DC.] Woods and thickets, St. Thomas; St. Jan; St. Croix.

MAYTENUS CYMOSA Krug & Urban. [*M. elaeodendroides* of Eggers.] Thickets, St. Thomas; St. Croix. Known otherwise only from Vieques. Endemic.

RHACOMA CROSSOPETALON L. [*Myginda pallens* Sw.; *M. latifolia* Vahl, not Sw.] Thickets, St. Thomas; St. Jan; St. Croix.

MYGINDA LATIFOLIA (Sw.) Urban. [*Myginda latifolia* Sw.] Thickets, St. Thomas.

SCHAEFFERIA FRUTESENS Jacq. [*S. completa* Sw.] Thickets, St. Thomas; St. Jan; St. Croix.

ELAEODENDRON XYLOCARPUM (Vahl) Urban. [*Cassine xylocarpa*

Vent.; *Celastrus polygamus* Vahl; *Rhamnus polygamus* West.] Coastal thickets, St. Thomas; St. Jan; St. Croix.

## HIPPOCRATEACEAE

HIPPOCRATEA VOLUBILIS L. is doubtfully accredited to St. Thomas by Urban (Symb. Ant. 4: 367).

## SAPINDACEAE

SERJANIA POLYPHYLLA (L.) Schum. [*Paullinia polyphylla* L.; *S. lucida* Schum.; *Paullinia curassavica* of West.] Woods and thickets, St. Thomas; St. Jan; St. Croix.

PAULLINIA PINNATA L. St. Thomas (according to Radlkofer).

Dr. Millspaugh records *Paullinia frutescens glabrescens* (L.) Radlk. from Midland, St. Croix, as perhaps cultivated.

CARDIOSPERMUM HALICACABUM L. Banks and thickets, spontaneous after cultivation, St. Thomas; St. Croix.

CARDIOSPERMUM MICROCARPUM H.B.K. Thickets, St. Thomas; St. Jan; St. Croix.

CARDIOSPERMUM CORINDUM L. Hillsides, St. Croix.

CARDIOSPERMUM BIPINNATUM West, is not known to modern botanists.

ALLOPHYLUS OCCIDENTALIS (Sw.) Radlk. [*Schmeidelia occidentalis* Sw.] Forests, St. Croix.

SAPINDUS SAPONARIA L. [*S. inaequalis* DC.] Forests, St. Thomas; St. Jan; St. Croix.

MELICOCCA BIJUGA L. Hillsides, woods and along roads, St. Thomas; St. Jan; St. Croix. Planted and naturalized.

CUPANIA TRIQUETRA A. Rich. [*C. fulva* of Eggers.] Woods and hills, St. Thomas; St. Jan.

BLIGHIA SAPIDA Koen. Planted for its fruit.

## DODONAEACEAE

DODONAEA VISCOSA L. Coastal thickets, St. Thomas; St. Croix.

## RHAMNACEAE

KRUGIODENDRON FERREUM (Vahl) Urban. [*Rhamnus ferreus* Vahl; *Ceanothus ferreus* DC.; *Condalia ferrea* Griseb.] Woods and thickets, St. Thomas; St. Jan; St. Croix.

REYNOSIA UNCINATA Urban. [*R. mucronata* of Eggers.] Coastal thickets near Tague Bay, St. Croix.

REYNOSIA GUAMA Urban. [*R. latifolia* of Eggers.] Hillside thickets, St. Thomas; St. Jan. Endemic.

SARCOMPHALUS RETICULATUS (Vahl) Urban. [*Paliurus reticulatus* Vahl; *Zizyphus reticulatus* Vahl.] Thickets, Fair Plain, St. Croix.

COLUBRINA COLUBRINA (Jacq.) Millsp. [*Rhamnus Colubrina* Jacq.; *Colubrina ferruginosa* Brongn.] Coastal thickets and hillsides, St. Thomas; St. Jan; St. Croix.

COLUBRINA RECLINATA (L'Her.) Brongn. [*Rhamnus reclinatus* L'Her.; *R. ellipticus* Sw.] Woods and thickets, St. Thomas; St. Jan; St. Croix.

GOUANIA LUPULOIDES (L.) Urban. [*Banisteria lupuloides* L.; *Gouania domingensis* L.] Woods and thickets, St. Thomas; St. Jan; St. Croix.

ZIZYPHUS JUJUBA (L.) Lam. [*Rhamnus Jujuba* L.] Planted for its fruit.

RHAMNUS GLABRATUS West. A species not understood by modern botanists.

## VITACEAE

VITIS TILIIFOLIA H. & B. [*V. caribaea* DC.] Forests, St. Thomas.

VITIS VINIFERA L. Planted for its fruit.

CISSUS SICYOIDES L. Woods, walls and thickets, St. Thomas; St. Jan; St. Croix.

CISSUS TRIFOLIATA L. [*C. acida* L.] Dry thickets, St. Thomas; St. Jan; St. Croix.

CISSUS CAUSTICA Tuss. [*C. trifoliata* of Eggers and of Millspaugh.] On trees and rocks, St. Thomas; St. Croix.

CISSUS OBOVATA Vahl. St. Croix. Known otherwise from St. Martin and eastern Porto Rico.

## TILIACEAE

CORCHORUS ACUTANGULUS L. Waste and cultivated grounds, St. Thomas; St. Croix.

CORCHORUS SILIQUOSUS L. Thickets, fields, waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

CORCHORUS HIRTUS L. Gardens and roadsides, St. Thomas and St. Croix (according to Eggers).

CORCHORUS HIRSUTUS L. Coastal thickets and hillsides, St. Thomas; St. Jan; St. Croix.

TRIUMFETTA EXCISA Urban. Bassin yard, St. Croix. Known otherwise only from Porto Rico.

TRIUMFETTA RHOMBOIDEA Jacq. Thickets, St. Croix.

TRIUMFETTA SEMITRILOBA Jacq. [*T. althaeoides* Lam.; *T. semitriloba havanensis* Millsp.] Woods, banks and thickets, St. Thomas; St. Jan; St. Croix.

TRIUMFETTA LAPPULA L. Thickets, St. Thomas; St. Jan; St. Croix.

SLOANEA DENTATA L. Planted on St. Croix (according to West).

## MALVACEAE

ABUTILON UMBELLATUM (L.) Sweet. [*Sida umbellata* L.] Rocky thickets and hillsides, St. Thomas; St. Jan; St. Croix.

ABUTILON HIRTUM (Lam.) Sweet. [*Sida hirta* Lam.; *Abutilon indicum hirtum* Griseb.; *A. graveolens* of Millspaugh.] Waste and cultivated grounds, St. Thomas; St. Croix.

ABUTILON INDICUM (L.) Sweet. [*Sida indica* L.; *A. subpapyraceum* Hochreutiner.] Sandy waste grounds, St. Thomas; St. Croix.

ABUTILON LIGNOSUM A. Rich. St. Thomas and St. Croix (according to Eggers).

GAYOIDES CRISPUM (L.) Small. [*Sida crispa* L.; *Abutilon crispum* Medic.] Sandy soil, St. Thomas.

WISSADULA AMPLISSIMA (L.) R. E. Fries. [*Sida amplissima* L.; ? *Abutilon periplocifolium albicans* of Eggers; *Sida hernandioides* L'Her.; *W. hernandioides* Garcke.] Banks and thickets, St. Jan; St. Croix.

WISSADULA PERIPLOCIFOLIA (L.) Griseb. [*Sida periplocifolia* L.; *Abutilon periplocifolium* Don.] Fields and hillsides, St. Croix.

MALVASTRUM COROMANDELIANUM (L.) Garcke. [*Malva coromandeliana* L.; *M. americana* L.; *M. tricuspidata* Ait.; *Malvastrum tricuspidatum* A. Gray.] Waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

MALVASTRUM SPICATUM (L.) A. Gray. [*Malva spicata* L.] Hillsides, waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

SIDA CILIARIS L. Dry, grassy and rocky situations, St. Thomas; St. Jan; St. Croix.

SIDA ERECTA Macf. Dry soil, St. Croix.

SIDA SPINOSA L. [*S. angustifolia* Lam.; (?) *S. spinosa polycarpa* Eggers; *S. retusa* of Millspaugh.] Banks, fields and cultivated grounds, St. Thomas; St. Jan; St. Croix.

SIDA GLOMERATA Cav. Banks and thickets, St. Thomas; St. Jan.

SIDA CARPINIFOLIA L. f. [*S. carpinifolia acuta* Millsp.; *S. carpinifolia antillana* Millsp.; (?) *S. carpinifolia brevicuspidata* Eggers.] Banks, fields, woods and thickets, St. Thomas; St. Jan; St. Croix.

SIDA RHOMBIFOLIA L. [*S. rhombifolia retusa* of Eggers.] Banks, fields, waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

SIDA PROCUMBENS Sw. [*S. pilosa* Cav.; *S. supina* Sw.] Roadsides, St. Croix.

SIDA CORDIFOLIA L. [*S. althaeifolia* Sw.; *S. cordifolia althaeifolia*

of Millspaugh.] Banks, fields and thickets, St. Thomas; St. Jan; St. Croix.

SIDA HUMILIS Cav. [*Sida supina* of Millspaugh, St. Thomas; *Sida supina glabra* of Millspaugh and of Eggers.] Banks, fields, and thickets, St. Thomas; St. Jan; St. Croix.

SIDA GLABRA Mill. [*S. ulmifolia* Cav.; *S. arguta* Sw.] Banks, fields and thickets, St. Thomas; St. Croix.

SIDA GLUTINOSA Commers. [*S. nervosa* DC.; (?) *S. nervosa viscosa* Eggers.] Hillsides and thickets, St. Thomas; St. Jan; St. Croix.

SIDA ACUMINATA DC. [*S. acuminata macrophylla* Schl. and *microphylla* Schl.] Hillsides, St. Thomas; St. Croix.

SIDA EGGERSII E. G. Baker. St. Thomas, apparently (Eggers, Suppl. 14). Otherwise known only from Tortola and Culebra. Endemic.

SIDA JAMAICENSIS L. [*S. tristis* Schl.] Fields and hillsides, St. Thomas; St. Jan; St. Croix.

BASTARDIA VISCOSA (L.) H.B.K. [*Sida viscosa* L.] Dry fields, hills and thickets, St. Thomas; St. Jan; St. Croix.

MALACHRA CAPITATA L. [*M. palmata* Moench.] Dry soil, St. Croix.

MALACHRA ALCEIFOLIA Jacq. [*M. rotundifolia* Schrank.] Thickets, waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

MALCHRA FASCIATA Jacq. [*M. radiata* Griseb., not L.; (?) *M. urens* of Eggers.] Waste grounds, St. Thomas.

URENA LOBATA L. [*U. americana* L. f.; *U. reticulata* Cav.; *U. lobata americana* Guerke.] Fields, woods, hillsides and cultivated grounds, St. Thomas; St. Jan; St. Croix.

URENA SINUATA L. St. Thomas (according to Guerke).

PAVONIA SPINIFEX (L.) Cav. [*Hibiscus spinifex* L.] Thickets, waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

MALACHE SCABRA B. Vogel. [*Pavonia spicata* Cav.; *Althaea racemosa* Sw.; *P. racemosa* Sw.] Mangrove swamps, St. Croix (according to Eggers).

PARITI TILIACEUM (L.) A. Juss. [*Hibiscus tiliaceus* L.] Coastal woods, St. Thomas; St. Jan; St. Croix (according to West).

HIBISCUS BRASILIENSIS L. [*H. phoeniceus* Jacq.] Hillsides and thickets, St. Thomas; St. Croix.

HIBISCUS CLYPEATUS L. St. Croix (according to West).

HIBISCUS VITIFOLIUS L. Thickets and waste grounds, St. Thomas; St. Croix.

HIBISCUS SABDARIFFA L. Spontaneous after cultivation, St. Thomas; St. Croix.

HIBISCUS ROSA-SINENSIS L. Spontaneous after cultivation, St. Thomas. Planted for ornament.

HIBISCUS MUTABILIS L. Planted for ornament.

CIENFUEGOSIA HETEROPHYLLA (Vent) Garcke. [*Fugosia heterophylla*; *Kosteletzkya pentasperma* of Eggers.] Moist soil, St. Thomas.

ABELMOSCHUS ESCULENTUS (L.) Moench. [*Hibiscus esculentus* L.] Spontaneous after cultivation, St. Thomas; St. Jan; St. Croix.

THESPESIA POPULNEA (L.) Soland. [*Hibiscus populneus* L.] Coastal woods and thickets, St. Thomas; St. Jan; St. Croix. Commonly planted.

GOSSYPIUM BARBADENSE L. Thickets and hillsides, spontaneous after cultivation, St. Thomas; St. Croix.

GOSSYPIUM VITIFOLIUM Lam. is recorded by Schlechtendal as naturalized in St. Thomas; Eggers suggests it may formerly have been cultivated there.

ALTHAEA ROSEA Cav. Planted for ornament.

## BOMBACACEAE

CEIBA PENTANDRA (L.) Gaertn. [*Bombax pentandrum* L.; *B. heptaphyllum* of West; *Eriodendron anfractuosum* DC.] Hills, forests and roadsides, St. Thomas; St. Jan; St. Croix.

ADANSONIA DIGITATA L. Naturalized in wooded valleys, St. Croix (according to Eggers). Planted for shade on St. Thomas and St. Croix.

QUARARIBAEA TURBINATA (Sw.) Poir. [*Myrodia turbinata* Sw.] Woods, St. Jan; Spring Garden, St. Croix (according to West).

PACHIRA ALBA Walp. Planted, St. Thomas.

PACHIRA AQUATICA Aubl. [*Carolinea princeps* L. f.] Planted, St. Croix.

## STERCULIACEAE

MELOCHIA NODIFLORA Sw. [*Riedleia nodiflora* DC.] Hillsides, banks and thickets, St. Thomas; St. Jan; St. Croix.

**Moluchia pyramidata** (L.) Britton. [*Melochia pyramidata* L.] Grassy places, waste and cultivated grounds, St. Thomas (according to West); St. Croix.

**Moluchia tomentosa** (L.) Britton. [*Melochia tomentosa* L.] Hillsides and thickets, St. Thomas; St. Jan; St. Croix.

WALTHERIA AMERICANA L. [*W. indica* L.] Fields, banks and hillsides, St. Thomas; St. Jan; St. Croix.

AYENIA PUSILLA L. Thickets and hillsides, St. Thomas; St. Jan; St. Croix.

THEOBROMA CACAO L. Naturalized in shaded valleys, St. Croix (according to Eggers). Planted for its seeds.

GUAZUMA GUAZUMA (L.) Cockerell. [*Theobroma Guazuma* L.;

*Guazuma ulmifolia* Lam.; *G. tomentosa* H.B.K.] Fields, woods and roadsides, St. Thomas; St. Croix.

Helicteres jamaicensis Jacq. Thickets, St. Thomas; St. Jan; St. Croix.

## DILLENIACEAE

Davilla rugosa Poir. is recorded by Grisebach from the island St. Thomas, and also from St. Thomas-in-the-Vale, Jamaica. It occurs in the Jamaica parish, but is not known on our island.

## OCHNACEAE

Ouratea littoralis Urban. [*Gomphia nitida* of Eggers.] Coastal thickets, St. Thomas. Known otherwise only from Porto Rico.

## TERNSTROEMIACEAE

**Taonabo peduncularis** (DC.) Britton. [*Ternstroemia peduncularis* DC.; *T. elliptica* of West and of Eggers.] Forests, Bordeaux Hill, St. Jan; Maroon Hill, St. Croix.

## CLUSIACEAE

Mammea americana L. Forests, hills and roadsides, St. Thomas; St. Jan; St. Croix. Much planted.

Calophyllum Calaba Jacq. Forests, roadsides and valleys, St. Thomas; St. Croix.

Clusia rosea Jacq. [? *C. alba* of West.] Hillsides and forests, St. Thomas; St. Jan; St. Croix (according to West and to Eggers).

## TAMARICACEAE

Tamarix indica Willd. Planted for ornament.

## BIXACEAE

Bixa Orellana L. Spontaneous after planting, St. Thomas; St. Croix. Grown for the dye stuff annato.

## CANELLACEAE

Canella Winterana (L.) Gaertn. [*Laurus Winterana* L.; *Canella alba* Murr.] Woods and thickets, St. Thomas; St. Jan; St. Croix (according to Eggers).

## VIOLACEAE

**Calceolaria linearifolia** (Vahl) Britton. [*Viola linearifolia* Vahl; *Hybanthus linearifolius* Urban; *Ionidium strictum* Vent.] Rocky thickets, Water Island, St. Thomas; St. Croix.

## FLACOURTIACEAE

PROCKIA CRUCIS L. [*Trilix crucis* Griseb.] Forests, St. Thomas; St. Jan (according to Eggers); St. Croix.

MYROXYLON BUXIFOLIUM (A. Gray) Krug & Urban. [*Xylosma buxifolium* A. Gray; *Drypetes laevigata* of Eggers.] Cinnamon Gut, St. Jan; St. Croix (according to Urban).

MYROXYLON NITIDUM (Hell.) Kuntze [*Xylosma nitidum* A. Gray], is recorded by Eggers as naturalized on St. Thomas. It is endemic in Jamaica.

SAMYDA SPINULOSA Vent. [*S. glabrata* Grisebach and of Eggers, not Sw.] Thickets, Crown, St. Thomas (according to Eggers). Otherwise known only from Porto Rico.

SAMYDA DODECANDRA Jacq. [*S. serrulata* L.] Thickets, St. Thomas; St. Jan; St. Croix.

CASEARIA GUIANENSIS (Aubl.) Urban. [*Iroucana guianensis* Aubl.; *Casearia ramiflora* Vahl; *C. hirta* of Millspaugh; *C. nitida* of Kuntze.] Woods and thickets, St. Thomas; St. Croix; St. Jan.

CASEARIA DECANDRA Jacq. [*C. parvifolia* Willd.; *Samyda decandra* Jacq.; *C. parvifolia microcarpa* Eggers.] Woods and thickets, St. Thomas; St. Jan; St. Croix (according to Eggers).

CASEARIA ARBOREA (L. C. Rich) Urban. [*Samyda arborea* L. C. Rich; *C. stipularis* Vent.] St. Thomas, collected by O. Kuntze, whose specimen is so labelled by him; Urban (Symb. Ant. 7: 75) indicates, however, that it may have come from Porto Rico.

CASEARIA SYLVESTRIS Sw. [*Samyda parviflora* L. not Loefl.] Woods, hills and thickets, St. Thomas; St. Jan; St. Croix.

## TURNERACEAE

TURNERA DIFFUSA Willd. [*T. microphylla* Desv.; *T. parviflora* of Eggers.] Coastal thickets, St. Thomas; St. Jan; St. Croix.

TURNERA ULMIFOLIA L. [*T. ulmifolia acuta* Urban; *T. angustifolia* Mill.] Hillsides and waste grounds, St. Thomas; St. Jan; St. Croix.

PIRIQUETA VISCOSA Griseb. Hillside thickets, St. Thomas.

## PASSIFLORACEAE

PASSIFLORA PALLIDA L. [*P. suberosa* L.; *P. hirsuta* L.; *P. minima* L.; *P. parviflora* Sw.; *P. peltata* Cav.] Hillsides, banks and thickets, St. Thomas; St. Jan; St. Croix.

PASSIFLORA FOETIDA L. Banks, waste and cultivated grounds, St. Thomas; St. Croix.

PASSIFLORA MULTIFLORA L. Thickets, St. Thomas (according to Masters); St. Jan.

PASSIFLORA RUBRA L. Woods and thickets, St. Thomas; St. Jan; St. Croix (according to Eggers).

PASSIFLORA LAURIFOLIA L. Forests and thickets, St. Thomas; St Jan; St. Croix. Perhaps not indigenous; much planted.

PASSIFLORA INCARNATA L., recorded from St. Croix by West, must be an error in determination.

PASSIFLORA QUADRANGULARIS L. Planted for its fruit.

PASSIFLORA MALIFORMIS L. Planted for its fruit.

## CARICACEAE

CARICA PAPAYA L. Spontaneous after cultivation, St. Thomas; St. Croix. Much planted.

## BEGONIACEAE

Several kinds of Begonias are grown as garden flowers.

BEGONIA HUMILIS Ait., attributed to St. Thomas by A. de Candolle as collected by Finlay, was really from Trinidad.

## CACTACEAE

HYLOCEREUS TRIGONUS (Haw.) Safford. [*Cereus trigonus* Haw.; *C. triangularis* of West and of Eggers.] On trees and rocks in forests and valleys, St. Thomas; St. Jan.

HYLOCEREUS UNDATUS (Haw.) Britton & Rose. [*Cereus undatus* Haw.; *Cereus triangularis* of authors.] Persistent after cultivation, St. Thomas; St. Croix.

SELENICEREUS GRANDIFLORUS (L.) Britton & Rose. [*Cereus grandiflorus* L.] Persistent after cultivation, St. Thomas; St. Croix.

SELENICEREUS PTERANTHUS (Link & Otto) Britton & Rose. [*Cereus nycticalis* Link.] Recorded by Millspaugh as naturalized on stone walls of a neglected garden at Bassin, St. Croix.

CEPHALOCEREUS ROYENI (L.) Britton & Rose. [*Cactus Royeni* L.; *C. peruvianus* of West; *Cereus floccosus* Otto; *Pilocereus Fouchianus* Weber; *Cereus armatus* Otto.] Dry rocky hillsides, St. Thomas; St. Jan; St. Croix.

CEPHALOCEREUS NOBILIS (Haw.) Britton & Rose. [*Cereus nobilis* Haw.; *Cereus strictus* DC.] Persistent after cultivation, St. Thomas.

ACANTHOCEREUS PENTAGONUS (L.) Britton & Rose. [*Cactus pentagonus* L.] Persistent after planting, St. Thomas; St. Croix.

CACTUS INTORTUS Mill. [*C. Melocactus* of West; *Melocactus communis* of Eggers; *M. atrosanguineus* Link & Otto.] Coastal hills and cliffs, St. Thomas; St. Jan; St. Croix.

CORYPHANTHA NIVOSA (Link) Britton. [*Mamillaria nivosa* Link.]

Rocky slopes and cliffs, Buck Island and Flat Cays, St. Thomas; St. Jan and Little St. James Island, St. Jan.

OPUNTIA RUBESCENS Salm-Dyck. [*O. catacantha* Link & Otto; *O. spinosissima* and *tuberculata* of Eggers.] Coastal hills, St. Thomas; St. Jan; St. Croix. The spineless or nearly spineless race is commonly planted for interest, and occurs wild on Little St. James Island, St. Jan, and on Culebra.

OPUNTIA REPENS Bello. [*Cactus curassavicus* of West; *O. curassavica* of Eggers and of Millspaugh.] Dry fields and hillsides, St. Thomas; St. Jan; St. Croix.

**Opuntia antillana** Britton & Rose, spec. nov.

Plant depressed, ascending or nearly prostrate, often forming clumps 1 m. broad, seldom more than 4 dm. high. Joints obovate or oblong-obovate, 2 dm. long or less, green, glabrous, readily detached; leaves conic-subulate, 2–3 mm. long; areoles large, 2–3 cm. apart, brown-woolly; spines mostly 3–6 at each areole, subulate, rather stout, terete, 1–6 cm. long, yellow fading gray or nearly white; glochids many, yellow; flowers about 7 cm. broad; petals obtuse, bright yellew or fading reddish; fruit red-purple, about 4 cm. long.

Rocky and sandy soil, St. Thomas, St. Croix, also on Tortola, Porto Rico, Hispaniola, and St. Kitts. Type specimen collected on St. Kitts (*Rose, Fitch & Russell 3230*).

OPUNTIA DILLENII (Ker.) Haw. [*Cactus Dillenii* Ker.; *Cactus Opuntia* of West; *O. Tuna* of Eggers and of Millspaugh; *O. horrida* Salm-Dyck.] Banks, fields and hills, St. Thomas; St. Jan; St. Croix. A hybrid with *O. rubescens* was observed on Buck Island, St. Thomas.

OPUNTIA TRIACANTHA (Willd.) DC. [*Cactus triacanthus* Willd.] Coastal rocks, Buck Island, St. Thomas.

NOPALEA COCHENILLIFERA (L.) Salm-Dyck. [*Cactus cochenillifer* L.; *Opuntia coccinellifera* Mill.] Persistent or spontaneous after cultivation; recorded by Eggers as occurring on limestone, St. Thomas; St. Croix.

PERESKIA PERESKIA (L.) Karst. [*Cactus Pereskia* L.; *P. aculeata* Mill.] Spontaneous after cultivation, St. Thomas; St. Croix.

PERESKIA GRANDIFOLIA Haw. [*P. Bleo* of Eggers and of Millspaugh.] Spontaneous after cultivation, St. Thomas; St. Croix.

CEREUS NORTHUMBERLANDIA Lambert. [*C. lepidotus* Salm-Dyck.] Planted, St. Croix.

CEREUS HEXAGONUS (L.) Mill. [*C. peruvianus* (L.) Mill.] Planted (according to Eggers).

Other species of Cacti are occasionally cultivated for interest.

## THYMELAEACEAE

Daphnopsis caribaea Griseb. [*Nectandra antillana* of Millspaugh.] Forests and hillsides, St. Thomas; St. Jan; St. Croix.

## LYTHRACEAE

Ammannia coccinea Rottb. Moist ground, St. Thomas; St. Jan; St. Croix.

Ammannia latifolia L. [*A. sanguinolenta* Sw.] Moist ground, St. Thomas; St. Croix.

Ginoria Rohrii (Vahl) Koehne. [*Antherylium Rohrii* Vahl.] Coastal thickets, St. Thomas; St. Jan; St. Croix.

Lawsonia inermis L. Spontaneous after cultivation, St. Thomas; St. Croix.

Lagerstroemia indica L. Commonly planted for ornament.

## PUNICACEAE

Punica Granatum L. [*P. nana* L.] Spontaneous after planting, St. Thomas; St. Jan; St. Croix. Grown for its fruit.

## RHIZOPHORACEAE

Rhizophora Mangle L. Mangrove swamps, St. Thomas; St. Jan; St. Croix. Not very common.

## COMBRETACEAE

Terminalia Catappa L. [*Buceras Catappa* Hitchc.] Hillsides, valleys, and commonly planted, St. Thomas; St. Jan; St. Croix.

Conocarpus erecta L. [*C. erecta procumbens* Jacq.] Coastal rocks and mangrove swamps, St. Thomas; St. Jan; St. Croix.

Bucida Buceras L. [*Buceras Buceras* Millsp.; *Myrobalanus Buceras* Kuntze.] Moist soil, mostly near the coasts, but occasional on hillsides, St. Thomas; St. Jan; St. Croix.

Laguncularia racemosa (L.) Gaertn. [*Conocarpus racemosa* L.] Coastal swamps, St. Thomas; St. Jan; St. Croix.

Quisqualis indica L. is commonly cultivated as an ornamental vine.

## MYRTACEAE

Psidium Guajava L. Thickets, hillsides, and commonly planted for its fruit, St. Thomas; St. Jan; St. Croix.

Psidium amplexicaule Pers. [*P. cordatum* Sims.] Hillsides, St. Thomas; St. Jan; planted on St. Croix. Occurs also on Tortola. Apparently endemic in the Virgin Islands, although recorded from Nevis.

PSIDIUM AROMATICUM Knox, recorded from St. Thomas, is not identified.

AMOMIS CARYOPHYLLATA (Jacq.) Krug & Urban. [*Myrtus caryophyllata* Jacq.; *Myrtus acris* Sw.; *M. Pimenta* Ortega; ? *Pimenta vulgaris* of Eggers; *Pimenta acris* Kostel.; *A. caryophyllata grisea* Krug & Urban.] Hills and woods, St. Jan; St. Croix (according to Eggers).

MYRCIA PANICULATA (Jacq.) Krug & Urban. [*Eugenia paniculata* Jacq.; *E. acetosans* Poir.; *E. marginata* Pers.; *Myrtus coriacea* Vahl; *Myrcia coriacea* DC.; *M. coriacea Imrayana* Griseb.] Forests, St. Thomas; St. Jan; St. Croix.

MYRCIA SPLENDENS (Sw.) DC., doubtfully accredited to St. Thomas by Urban, as collected by Riedlé, probably was from Porto Rico, where it is abundant.

CALYPTRANTHES THOMASIANA Berg. Signal Hill, St. Thomas; Bordeaux, St. Jan. Endemic.

CALYPTRANTHES PALLENS (Poir.) Griseb. [*C. Chytraculia ovalis* Berg.; *C. Chytraculia zuzygium* Berg.; *Chytraculia pallens* Millsp.; *C. Chytraculia* of West.] Forests, rare, St. Thomas; St. Croix.

EUGENIA LIGUSTRINA (Sw.) Willd. [*Myrtus ligustrina* Sw.; *M. cerasina* Vahl.] Woods and thickets, St. Thomas; St. Jan; St. Croix.

EUGENIA LANCEA Poir. [*E. ludibunda* Bert.; *E. virgultosa* of Eggers and of Millspaugh; *E. glabrata* of Eggers; *Myrcia thomasiana* DC.] Woods and thickets, St. Thomas; St. Croix.

EUGENIA MONTICOLA (Sw.) DC. [*Myrtus monticola* Sw.; *Eugenia Poiretii* Berg, not DC.; *E. foetida* West; *E. flavovirens* Berg.] Woods and thickets, St. Thomas; St. Jan; St. Croix.

EUGENIA BUXIFOLIA (Sw.) Willd. [*Myrtus buxifolia* Sw.; *E. foetida* Poir.] Thickets, St. Thomas; St. Croix.

EUGENIA AXILLARIS (Sw.) Willd. [*Myrtus axillaris* Sw.] Thickets, St. Croix.

EUGENIA RHOMBEA (Berg) Krug & Urban. [*E. foetida rhombea* Berg.; *E. Poiretii* of Millspaugh; ? *E. pallens* of Eggers.] Coastal thickets, St. Thomas (according to Berg); St. Croix.

EUGENIA PROCERA (Sw.) Poir. [*Myrtus procera* Sw.; *M. cerasina* Vahl of Eggers.] Woods and thickets, St. Thomas; St. Jan; St. Croix.

EUGENIA PSEUDOPSIDIUM Jacq. [*E. portoricensis* DC.; *E. thomasiana* Berg.] Forests and wooded valleys, St. Thomas; St. Jan; St. Croix.

EUGENIA CORDATA (Sw.) DC. [*Myrtus cordata* Sw.; *M. ramiflorus* Vahl; *E. sessiliflora* DC., not Vahl; *E. lateriflora* of Eggers.] Woods and thickets, St. Thomas; St. Jan; St. Croix.

Eugenia sessiliflora Vahl. Hillsides, St. Thomas (according to Eggers); St. Croix. Endemic.

Eugenia floribunda West. Woods, hillsides and thickets, St. Thomas; St. Jan; St. Croix.

Eugenia uniflora L. Spontaneous after planting, St. Thomas; St. Croix. Grown for its fruit.

Eugenia micrantha Vahl, not DC., recorded from St. Croix by West, is not further determined (hyponym).

Eugenia emarginata Vahl, not DC., recorded from St. Croix by Vahl, is not further determined (hyponym).

Eugenia pedunculata Raeusch. of St. Croix, is unknown to modern botanists.

Anamomis fragrans (Sw.) Griseb. [*Myrtus fragrans* Sw.; *Eugenia punctata* Vahl; *Anamomis punctata* Griseb.] St. Croix; forests, St. Jan (according to Eggers).

Jambos Jambos (L.) Millsp. [*Eugenia Jambos* L.; *Jambos vulgaris* DC.] Woods and valleys, naturalized, St. Thomas; St. Jan; St. Croix.

Jambos malaccensis (L.) DC. [*Eugenia malaccensis* L.], planted for its fruit, was naturalized in shaded valleys, St. Croix (according to Eggers).

Myrtus communis L. Planted for ornament.

## LECYTHIDACEAE

Couroupita guianensis Aubl. Planted for ornament and interest.

## MELASTOMACEAE

Tetrazygia angustifolia (Sw.) DC. [*Melastoma angustifolia* Sw.; *Miconia angustifolia* Griseb.] Hillside thickets, St. Thomas; St. Jan; St. Croix (according to Cogniaux).

Tetrazygia elaeagnoides (Sw.) DC. [*Melastoma elaeagnoides* Sw.] Forests and hillside thickets, St. Thomas; St. Jan; St. Croix.

Miconia macrophylla (D. Don) Triana. [*Chitonia macrophylla* D. Don; *Diplochita serrulata* DC.] Wooded valleys, St. Thomas; St. Croix (according to Eggers and to Cogniaux).

Miconia impetiolaris (Sw.) D. Don. [*Melastoma impetiolaris* Sw.] Forests, St. Croix (West); St. Thomas (according to Grisebach).

Miconia laevigata (L.) DC. [*Melastoma laevigata* L.; *M. prasina* of Millspaugh, St. Thomas.] Woods and hillsides, St. Thomas; St. Jan; St. Croix.

Miconia prasina (Sw.) DC., recorded by Naudin as collected on

St. Thomas by Riedlé, was probably from Porto Rico. It occurs on Tortola.

MICONIA STENOSTACHYA (Schr.) DC. [*Miconia argyrophylla* Benth., not DC.], recorded by Naudin and others as collected by Finlay on St. Thomas, was really from Trinidad.

MICONIA THOMASIANA DC. was not from St. Thomas, but from Porto Rico.

MICONIA ACINODENDRUM (L.) Triana. [*Melastoma acinodendrum* L.; *Tshudya berbiceana* Griseb.], recorded by Naudin and others as collected on St. Thomas by Finlay, was really from Trinidad; St. Croix (according to West).

MECRANIUM AMYGDALINUM (Desr.) C. Wright [*Cremanium amygdalinum* Griseb.], attributed to St. Thomas by Naudin, was from Hispaniola, collected by Poiteau.

CLIDEMIA SPICATA DC., is recorded by Cogniaux as collected on St. Thomas by Finlay, but the specimen was from Trinidad. Eggers erroneously records it from all three islands.

CLIDEMIA HIRTA (L.) D. Don, attributed to St. Thomas by Naudin as collected by Riedlé, was probably from Porto Rico.

CLIDEMIA RUBRA Mart, accredited to St. Thomas by Naudin and others as collected by Finlay, was really from Trinidad.

MOURIRIA DOMINGENSIS (Tuss.) Spach. [*Petaloma domingensis* Tuss.; *P. Mouriri* of West.] Borders of a stream, Spring Garden, St. Croix.

NEPSERA AQUATICA (Aubl.) Naud., recorded by Cogniaux as collected by Riedlé on St. Thomas, was probably from Porto Rico.

## ONAGRACEAE

JUSSIAEA SUFFRUTICOSA L. [*J. angustifolia* Lam.; *J. octovalvis* Sw.; *J. suffruticosa ligustrifolia* of Eggers.] Wet grounds, St. Thomas; St. Jan; St. Croix.

JUSSIAEA ERECTA L. St. Croix (according to West).

## ARALIACEAE

DENDROPANAX ARBOREA (L.) Dcne. & Pl. [*Sciadophyllum capitatum* of Eggers; *Aralia arborea* L.; *Gilibertia arborea* E. March.] Forests, hills of St. Thomas.

DIDYMOPANAX MICANS (Willd.) Krug & Urban. [*Aralia micans* Willd.; *Panax speciosum* of Eggers.] Forest, King's Hill and Bordeaux, St. Jan.

## APIACEAE

ERYNGIUM FOETIDUM L. Moist grounds, Caret Bay, St. Thomas (according to Eggers).

CELERI GRAVEOLENS (L.) Britton. [*Apium graveolens* L.; *Peucedanum graveolens* Benth.] Persistent after cultivation, St. Croix. Grown for celery.

ANETHUM GRAVEOLENS L. Spontaneous after cultivation, St. Thomas; St. Croix.

PIMPINELLA ANISUM L. Spontaneous after cultivation, St. Croix. Grown for anise.

APIUM PETROSELINUM L. [*Petroselinum sativum* Hoffm.] Cultivated for food.

DAUCUS CAROTA L. Cultivated for food.

FOENICULUM FOENICULUM (L.) Karst. [*F. vulgare* Gaertn.] Cultivated for drug purposes.

CEREFOLIUM CEREFOLIUM (L.) Britton. [*Anthriscus Cerefolium* L.] Cultivated for flavoring.

## ERICACEAE

XOLISMA RUBIGINOSA (Pers.) Small. [*Andromeda rubiginosa* Pers.; *Lyonia jamaicensis* of Eggers.] Bolongo, St. Thomas. Known otherwise only from Hispaniola.

## THEOPHRASTACEAE

JACQUINIA BERTERII Spreng. [*J. Berterii retusa* Urban.] Thickets, St. Thomas; St. Jan; St. Croix (according to Mez).

JACQUINIA BARBASCO (Loefl.) Mez. [*Chrysophyllum Barbasco* Loefl.; *J. armillaris* Jacq.; *J. armillaris arborea* of Eggers.] Coastal thickets, St. Thomas; St. Jan; St. Croix.

## MYRSINACEAE

ICACOREA GUADALUPENSIS (Duch.) Britton. [*Ardisia guadalupensis* Duch.; *A. coriacea* of West and of Eggers.] Forests and hills, St. Thomas; St. Jan; St. Croix.

STYLOGYNE LATERIFLORA (Sw.) Mez. [*Ardisia lateriflora* Sw.; *A. caribaea* Miquel.] St. Thomas (according to Eggers).

## PLUMBAGINACEAE

PLUMBAGO SCANDENS L. [*P. scandens densiflora* Kuntze.] Banks, woods and thickets, St. Thomas; St. Jan; St. Croix.

PLUMBAGO CAPENSIS Thunb. Grown in gardens.

PLUMBAGO ZEYLANICA L. St. Croix (according to West).

## SAPOTACEAE

SAPOTA ACHRAS Mill. [*Achras Sapota* L.] Forests, and commonly planted, St. Thomas; St. Jan; St. Croix.

LUCUMA MULTIFLORA A. DC. [*Achras multiflora* Vahl, according to Eggers.] Forests, St. Thomas; St. Croix.

SIDEROXYLON FOETIDISSIMUM Jacq. [*S. mastichodendron* Jacq.] Forests, St. Thomas; St. Jan; St. Croix.

DIPHOLIS SALICIFOLIA (L.) A. DC. [*Achras salicifolia* L.; *Bumelia salicifolia* Sw.] Forests and hillsides, St. Thomas; St. Jan; St. Croix.

BUMELIA OBOVATA (Lam.) A. DC. [*Sideroxylon obovatum* Lam.; *B. cuneata* Sw.] Coastal hillsides, shores and borders of marshes, St. Thomas; St. Jan; St. Croix.

CHRYSOPHYLLUM CAINITO L. St. Thomas; St. Croix, occasionally planted, perhaps spontaneous.

CHRYSOPHYLLUM EGGERSII Pierre. [*C. microphyllum* of Eggers; ? *C. oliviforme monopyrenum* of Eggers.] Woods and hillsides, St. Thomas; St. Jan; St. Croix. Endemic.

CHRYSOPHYLLUM PAUCIFLORUM Lam. [*C. glabrum* of Eggers and of Millspaugh; *C. pauciflorum nervosum* Pierre.] Forests and hillsides, St. Thomas; St. Jan; St. Croix. Otherwise known only from Porto Rico.

CHRYSOPHYLLUM BICOLOR Pierre. St. Thomas (according to Pierre and Urban); known otherwise only from Porto Rico.

MIMUSOPS NITIDA (Sessé & Moç.) Urban. [*Sapota Sideroxylon* of Eggers.] Forests, St. Jan. Determined from foliage only; its flowers and fruit have not been collected by botanists, and the identification is, therefore, uncertain.

MIMUSOPS ELENGI L. Planted, St. Thomas.

## SYMPLOCACEAE

SYMPLOCOS MARTINICENSIS Jacq. Forest, Signal Hill, St. Thomas.

## OLEACEAE

FORESTIERA SEGREGATA (Jacq.) Krug & Urban. [*Myrica segregata* Jacq.; *Forestiera porulosa* Poir; *F. porulosa Jacquinii* Eggers.] Thickets, St. Croix.

FORESTIERA EGGERSIANA Krug & Urban. Thickets, St. Thomas; St. Jan. Known otherwise only on Culebra, Vieques and Virgin Gorda, thus endemic in the Virgin Islands.

FORESTIERA RHAMNIFOLIA Griseb. [*Drypetes laevigata* of Millspaugh.] Bluffs of Salt River, St. Croix.

MAYEPAEA CARIBAEA (Jacq.) Kuntze. [*Chionanthus caribaea* Jacq.; *C. compacta* Sw.; *Linociera compacta* R. Br.] Forests, St. Thomas; St. Croix.

JASMINUM SAMBAC (L.) Soland. [*Nyctanthes Sambac* L.; *J. quinqueflorum* Heyne.] Spontaneous after planting, St. Croix.

JASMINUM PUBESCENS (Retz) Willd. [*Nyctanthes pubescens* Retz.] Spontaneous after planting, St. Thomas; St. Croix.

JASMINUM GRANDIFLORUM L. [*J. officinale* of Millspaugh.] Spontaneous after planting, St. Thomas; St. Croix.

JASMINUM OFFICINALE L. Planted for ornament.

JASMINUM HUMILE L. [*J. revolutum* Sims.] Planted for ornament.

OLEA EUROPAEA L. Planted on St. Thomas.

## LOGANIACEAE

SPIGELIA ANTHELMIA L. Moist or exsiccated situations, St. Thomas; St. Croix.

## APOCYNACEAE

ALLAMANDA CATHARTICA L. Spontaneous after cultivation, St. Thomas.

PLUMIERA ALBA L. Coastal rocks and hills, St. Thomas; St. Jan; St. Croix.

PLUMIERA RUBRA L. [*P. obtusifolia* of Millspaugh.] Planted for ornament.

PLUMIERA OBTUSA L. St. Croix (according to West); naturalized in gardens (according to Eggers).

CATHARANTHUS ROSEUS (L.) D. Don. [*Vinca rosea* L.; *Lochnera rosea* Rchb.] Waste grounds, spontaneous after cultivation, and much planted for ornament, St. Thomas; St. Jan; St. Croix.

TABERNAEMONTANA CAPENSIS L. Planted for ornament.

A species of *Tabernaemontana* was found in thickets at Frenchman's Bay, St. Thomas, according to Eggers, who, doubtfully, records it as *T. citrifolia*.

RAUWOLFIA TETRAPHYLLA L. [*R. nitida* Jacq.] Woods, hillsides and thickets, St. Thomas; St. Jan; St. Croix.

RAUWOLFIA LAMARCKII A. DC. Hillsides and thickets, St. Thomas; St. Jan; St. Croix.

CERBERA THEVETIA L. [*Thevetia Thevetia* Millsp.; *T. neriifolia* Juss.] Hillsides and thickets, St. Thomas; St. Jan; St. Croix.

ECHITES AGGLUTINATA Jacq. [*E. circinalis* Sw.] Forests and thickets, St. Thomas; St. Jan; St. Croix at Cane Bay (according to Eggers).

URECHITES LUTEA (L.) Britton. [*Vinca lutea* L.; *Echites suberecta* Jacq.; *E. barbata* Desv.; *E. neriandra* Griseb.] Thickets, St. Thomas; St. Jan; St. Croix (according to Eggers).

NERIUM OLEANDER L. Persistent after cultivation; planted for ornament; St. Thomas; St. Jan; St. Croix.

## ASCLEPIADACEAE

Asclepias curassavica L. [*A. nivea curassavica* Kuntze.] Fields, hillsides and banks, St. Thomas; St. Jan; St. Croix.

Asclepias nivea L. Collected on St. Thomas by Krebs.

Asclepias fruticosa L. Cultivated on St. Croix (according to West).

Calotropis procera (Ait.) Ait. f. [*Asclepias procera* Ait.] Fields and hillsides, St. Thomas; St. Jan; St. Croix. Naturalized.

Metastelma parviflorum R. Br. [*M. Schlechtendalii* of Eggers and of Millspaugh.] Thickets, St. Thomas; St. Croix.

Metastelma albiflorum Griseb. St. Thomas (according to Schlechter).

Metastelma decipiens Schlechter. St. Thomas (according to Schlechter).

Metastelma Grisebachianum Schlechter. St. Thomas. Otherwise known only from Porto Rico.

Metastelma Decaisneanum Schlechter. Hillsides, St. Thomas; St. Jan; St. Croix.

The above-listed species of *Metastelma* much resemble each other. It is possible that Schlechter has recognized too many species in the area.

Oxypetalum cordifolium (Vent) Schlechter. [*Gothofreda cordifolia* Vent.; *O. riparium* H.B.K.] St. Thomas (according to Schlechter).

Philibertella clausa (Jacq.) Vail. [*Asclepias viminalis* Sw.; *Sarcostemma Brownei* Meyer], recorded as from St. Thomas by West and by Eggers, has not been observed there by recent collectors.

Fischeria crispiflora (Sw.) Schltr. [*Cynanchum crispiflorum* Sw.; *F. scandens* DC.] Forests, Spring-gut, St. Croix (according to Eggers). Known otherwise only from Cuba and Jamaica; the determination is doubtful.

Ibatia maritima (Jacq.) Dcne. [*Asclepias maritima* Jacq.; *Ibatia muricata* Griseb.] Rocky hillsides and thickets, St. Thomas; St. Jan; St. Croix.

Hoya carnosa (L. f.) R. Br. Cultivated for ornament.

Stephanotis floribunda A. Brongn. Cultivated for ornament.

## CUSCUTACEAE

Cuscuta americana L. On trees and shrubs, St. Thomas; St. Jan; St. Croix.

## CONVOLVULACEAE

Evolvulus nummularius L. Dry, shaded situations, St. Thomas; St. Jan; St. Croix.

Evolvulus glaber Spreng. [*E. mucronatus* Sw.] Moist, grassy situations, St. Thomas; St. Jan; St. Croix.

Evolvulus linifolius L. St. Thomas and St. Croix (according to Schlechtendal); moist localities, all islands (according to Eggers). Not found by us, and not known on Porto Rico.

Jacquemontia nodiflora (Desr.) G. Don. [*Convolvulus nodiflorus* Desr.; *C. albiflorus* West (hyponym).] Thickets, St. Thomas; St. Jan; St. Croix.

Jacquemontia jamaicensis (Jacq.) Hall. f. [*Convolvulus jamaicensis* Jacq.] Coastal thickets, St. Thomas; St. Croix.

Jacquemontia pentantha (Jacq.) G. Don. [*Convolvulus pentanthus* Jacq.; *C. violaceus* Vahl; *J. violacea* Choisy.] Thickets, St. Thomas; St. Jan; St. Croix.

Convolvulus matutinus West and C. venenatus West, described from St. Croix, are not further identified.

Thyella tamnifolia (L.) Raf. [*Ipomoea tamnifolia* L.; *Jacquemontia tamnifolia* Griseb.] Banks, hills and thickets, St. Thomas; St. Jan (according to Eggers); St. Croix.

**Exogonium solanifolium** (L.) Britton. [*Ipomoea solanifolia* L.; *I. filiformis* Jacq.; *Convolvulus filiformis* Desr.; *Exogonium filiforme* Choisy; *Ipomoea eustachiana* of Millspaugh.] Coastal thickets, St. Thomas; St. Croix.

Exogonium repandum (Jacq.) Choisy. [*Ipomoea repanda* Jacq.] Woods and forests, St. Thomas; St. Jan.

Exogonium arenarium Choisy. [*Ipomoea arenaria* Steud.; *I. Steudelii* Millsp.; *I. Eggersiana* Peter; *E. Eggersii* House.] Thickets, St. Thomas; St. Jan; St. Croix.

Ipomoea dissecta (Jacq.) Pers. [*Convolvulus dissectus* Jacq.; *Merremia dissecta* Hall. f.; *Operculina dissecta* House; *Ipomoea sinuata* Ort.] Thickets, fences and woods, St. Thomas; St. Jan; St. Croix.

Ipomoea aegyptia L. [*Convolvulus pentaphyllus* L.; *Ipomoea pentaphylla* Jacq.; *Merremia aegyptia* Urban.] Fields, fences and thickets, St. Thomas; St. Jan; St. Croix.

Ipomoea quinquefolia L. [*Merremia quinquefolia* Hall. f.] Thickets, St. Thomas; St. Croix.

Ipomoea polyanthes R. & S. [*Convolvulus umbellatus* L.; *Ipomoea umbellata* Meyer, not L.; *Merremia umbellata* Hall. f.; *Ipomoea mollicoma* Miq.; *Convolvulus sagittifer* H.B.K.] Fields, banks and thickets, St. Thomas; St. Jan; St. Croix.

Ipomoea Nil (L.) Roth. [*Convolvulus Nil* L.; *Pharbitis Nil* Choisy; *I. hederacea barbata* of Kuntze; ? *Convolvulus hederaceus* of Schlechtendal.] Banks, waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

IPOMOEA CATHARTICA Poir. [*Convolvulus acuminatus* Vahl; *Ipomoea acuminata* R. & S., not R. & P.; *Pharbitis cathartica* Choisy; *P. acuminata* Choisy.] Woods and thickets, St. Thomas; St. Jan; St. Croix.

IPOMOEA ASARIFOLIA (Desr.) R. & S. [*Convolvulus asarifolius* Desr.] Danish Islands (according to Grisebach).

IPOMOEA PES-CAPRAE (L.) Roth. [*Convolvulus Pes-caprae* L.; *C. brasiliensis* L.; *C. maritimus* Lam.] Coastal sands, St. Thomas; St. Jan; St. Croix.

IPOMOEA STOLONIFERA (Cyr.) Poir. [*Convolvulus littoralis* L.; *C. arenarius* Vahl; *Ipomoea littoralis* Boiss.; *Convolvulus stoloniferus* Cyr.; *Ipomoea acetosaefolia* R. & S.] Coastal sands, St. Croix (according to West).

IPOMOEA HEPTAPHYLLA (Rottl. & Willd.) Voigt. [*Convolvulus heptaphyllus* Rottl. & Willd.; *Ipomoea pulchella* Griseb., not Roth.] St. Thomas (according to Urban).

IPOMOEA CARNEA Jacq. St. Croix (according to West).

IPOMOEA TRILOBA L. [*Convolvulus Sloanei* Spreng.; *I. parviflora* Vahl; *I. triloba eustachiana* of Eggers; *I. triloba quinqueloba* Kuntze.] Fields, banks and thickets, St. Thomas; St. Jan; St. Croix.

IPOMOEA TILIACEA (Willd.) Choisy. [*Convolvulus tiliaceus* Willd.; *C. fastigiatus* Roxb.; *I. fastigiata* Sweet; *I. Batatus fastigiata* Kuntze.] Thickets and hillsides, St. Thomas; St. Jan; St. Croix.

IPOMOEA BATATAS (L.) Lam. [*Convolvulus Batatas* L.; *Ipomoea pandurata cuspidata* Kuntze.] Persistent after cultivation, St. Thomas; St. Jan; St. Croix. Much planted for food.

IPOMOEA TRICOLOR Cav. [*I. violacea* Grisebach, and of Eggers and Millspaugh.] Woods and thickets, St. Thomas; St. Jan; St. Croix.

IPOMOEA PURPUREA (L.) Lam. [*Convolvulus purpureus* L.] St. Croix (according to West). Planted for ornament.

IPOMOEA LEARII Paxton. Planted for ornament.

IPOMOEA PES-TIGRIDIS L. [*Convolvulus Pes-tigridis* L.] St. Thomas (according to Schlechtendal).

IPOMOEA HORSFALLIAE W. Hook. Planted for ornament.

IPOMOEA QUINQUEPARTITA (Vahl) R. & S. [*Convolvulus quinquepartitus* Vahl; *C. ovalifolius* West, not Vahl,] of St. Croix, is not further identified.

IPOMOEA LEUCANTHA Jacq., a South American species, is recorded by Eggers from St. Thomas and St. Croix.

OPERCULINA TRIQUETRA (Vahl) Hallier f. [*Convolvulus triqueter* Vahl; *Ipomoea triquetra* R. & S.] St. Thomas; St. Croix.

OPERCULINA TUBEROSA (L.) Meissn. [*Ipomoea tuberosa* L.] Forests, St. Thomas; St. Croix (according to Eggers).

Calonyction aculeatum (L.) House. [*Convolvulus aculeatus* L.; *Ipomoea Bona-nox* L.] Spontaneous after cultivation, St. Thomas. Planted for ornament.

Calonyction tuba (Schlecht.) Colla. [*Convolvulus tuba* Schlecht.; *Ipomoea tuba* G. Don.] Coastal thickets, St. Thomas; St. Jan; St. Croix.

Quamoclit Quamoclit (L.) Britton. [*Ipomoea Quamoclit* L.; *Quamoclit vulgaris* Choisy.] Banks, thickets and cultivated grounds, St. Thomas; St. Croix.

Quamoclit coccinea (L.) Moench. [*Ipomoea coccinea* L.; *I. hederaefolia* L.; *I. sanguinea* Vahl.] Banks, thickets and cultivated grounds, St. Thomas; St. Jan; St. Croix.

Rivea tiliifolia (Desr.) Choisy. [*Convolvulus tiliifolius* Desr.; *Argyreia tiliifolia* Wright; *Convolvulus melanostictus* Schl.] Thickets, St. Thomas; St. Jan; St. Croix.

## POLEMONIACEAE

Phlox Drummondii Hook. Grown in flower gardens.

## HYDROPHYLLACEAE

Marilaunidium jamaicense (L.) Kuntze. [*Nama jamaicensis* L.; *Hydrolea jamaicensis* Vahl.] Dry, rocky situations, St. Thomas; St. Croix.

## CORDIACEAE

Cerdana alliodora R. & P. [*Cordia Gerascanthus* Jacq., not L.; *C. Gerascanthus subcanescens* of Eggers.] Woods and forests, St. Thomas; St. Jan.

Sebesten Sebestena (L.) Britton. [*Cordia Sebestena* L.; *C. Rickseckeri* Millsp.] Coastal thickets, hillsides, and planted for ornament, St. Thomas; St. Jan; St. Croix.

Sebesten brachycalyx (Urban) Britton. [*Cordia Sebestena brachycalyx* Urban.] Rocky hillside, Buck Island, St. Thomas. Known otherwise only from Porto Rico.

Cordia alba (Jacq.) R. & S. [*Varronia alba* Jacq.] Thickets and hillsides, St. Thomas; St. Croix. Sometimes planted.

Cordia collococca L. [*C. micrantha* Sw.] Woods, forests and hills, St. Thomas; St. Jan; St. Croix.

Cordia nitida Vahl. [? *C. laevigata* of Schlechtendal.] Forests and hills, St. Thomas; St. Jan; St. Croix.

Cordia sulcata DC. [*C. macrophylla* R. & S.] Forests and hills, St. Thomas; St. Jan; St. Croix (according to West).

Varronia corymbosa (L.) Desv. [*Lantana corymbosa* L.; *Cordia*

*ulmifolia* Juss.; *C. ulmifolia* and varieties of Eggers.] Thickets, fields and hillsides, St. Thomas; St. Jan; St. Croix.

Varronia angustifolia West. [*Cordia angustifolia* R. & S.; *C. cylindrostachya* and varieties of Eggers; *C. cylindrostachya* of Millspaugh.] Hillsides and thickets, St. Thomas; St. Croix (type locality).

Cordia martinicensis R. & S. is accredited to St. Croix by Grisebach (Fl. 481); the record probably refers to *V. angustifolia.*

Varronia globosa Jacq. [*Cordia globosa* H.B.K.] Thickets, St. Thomas and St. Croix (according to West, Schlechtendal and Eggers).

Bourreria succulenta Jacq. [*Ehretia Bourreria* L.] Forests, hillsides and thickets, St. Thomas; St. Jan; St. Croix.

Rochefortia acanthophora (DC.) Griseb. [*Ehretia acanthophora* DC.; (?) *Ehretia spinosa* Jacq.] Thickets, St. Thomas; St. Jan; St. Croix (according to West and to Eggers).

## BORAGINACEAE

Tournefortia filiflora Griseb. [*T. foetidissima* DC. and of Eggers, not L.] St. Jan (according to Eggers); St. Croix (according to West).

Tournefortia hirsutissima L. Thickets, banks and hills, St. Thomas; St. Jan; St. Croix.

Tournefortia bicolor Sw. [*T. laevigata* Lam.] Among rocks, Crown, St. Thomas.

Tournefortia laurifolia Vent., attributed to St. Thomas by Ventenat and by de Candolle, is known to us only from Porto Rico.

Tournefortia volubilis L. Thickets, St. Thomas; St. Jan; St. Croix (according to Eggers).

Tournefortia microphylla Bert. [*T. volubilis microphylla* DC.; *T. volubilis microcarpa* of Millspaugh.] Thickets, St. Thomas; St. Jan; St. Croix.

Mallotonia gnaphalodes (L.) Britton. [*Heliotropium gnaphalodes* L.; *Tournefortia gnaphalodes* R. Br.] Coastal sands, St. Thomas; St. Jan; St. Croix.

Heliotropium curassavicum L. Saline soil, St. Thomas; St. Jan; St. Croix.

Heliotropium parviflorum L. Banks, hillsides, waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

Heliotropium indicum L. Waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

Heliotropium ternatum Vahl. [*Heliotropium fruticosum* L.,

in part, and of Eggers and Millspaugh.] Rocky thickets and hillsides, St. Thomas; St. Jan; St. Croix.

HELIOTROPIUM PERUVIANUM L. Cultivated in flower gardens.

## VERBENACEAE

LANTANA CAMARA L. [*L. scabrida* Ait.] Thickets and hillsides, St. Thomas; St. Jan; St. Croix.

LANTANA ACULEATA L. [*L. polyacantha* Schauer.] Waste grounds, St. Thomas; St. Croix.

LANTANA INVOLUCRATA L. [*L. odorata* L.; *Camara involucrata* Kuntze.] Thickets and hillsides. St. Thomas; St. Jan; St. Croix.

LANTANA RETICULATA Pers. Stony ground, King's Hill, St. Croix (according to Eggers).

LIPPIA REPTANS H.B.K. [*Lippia nodiflora* of Eggers and of Millspaugh.] Wet ground, St. Croix.

LIPPIA TRIPHYLLA (L'Her.) Kuntze. [*Aloysia citriodora* Ort.] Cultivated in gardens.

BOUCHEA PRISMATICA (L.) Kuntze. [*Verbena prismatica* L.; *B. Ehrenbergii* Cham.] Waste and cultivated grounds, St. Thomas; St. Croix.

VALERIANODES JAMAICENSIS (L.) Medic. [*Verbena jamaicensis* L.; *Stachytarpheta jamaicensis* Vahl; *Valerianodes jamaicensis indicus* Kuntze.] Fields, hills, banks and in cultivated grounds, St. Thomas; St. Jan; St. Croix.

VALERIANODES STRIGOSA (Vahl) Kuntze. [*Stachytarpheta strigosa* Vahl.] Thickets and hillsides, St. Thomas; St. Jan.

PRIVA LAPPULACEA (L.) Pers. [*Verbena lappulacea* L.; *V. mexicana* of West; *P. echinata* Juss.] Waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

CITHAREXYLUM FRUTICOSUM L. [*C. cinereum* L.; *C. villosum* Jacq.] Woods, hills and thickets, St. Thomas; St. Jan; St. Croix.

CITHAREXYLUM SPINOSUM L. [*C. quadrangulare* Jacq.] Forests and slopes, St. Thomas; St. Croix. Planted for shade.

DURANTA ERECTA L. [*D. Plumieri* Jacq.; *D. Ellisia* Jacq.; ? *D. repens* L.] Thickets and hillsides, St. Thomas; St. Jan; St. Croix. Sometimes planted for ornament.

CALLICARPA RETICULATA Sw., accredited to St. Croix by West, is a little-known species of Jamaica; what plant West had in mind is not further recorded.

AEGIPHILA MARTINICENSIS Jacq. Forests, St. Thomas; St. Croix, common (according to Eggers).

PETITIA DOMINGENSIS Jacq. In forests, St. Croix, not common (according to Eggers).

VITEX DICARICATA Sw. Forests, St. Thomas; St. Jan; St. Croix (according to Eggers), and recorded from St. Croix by Swartz.

VITEX AGNUS-CASTUS L. Planted for ornament.

VOLKAMERIA ACULEATA L. [*Clerodendron aculeatum* Schlecht.; *C. aculeatum grandifolium* and *parvifolium* Kuntze; ? *C. longicollis* of Borgesen and Paulsen.] Thickets, St. Thomas; St. Jan; St. Croix.

CLERODENDRON FRAGRANS Vent. [*C. fragrans pleniflora* Schauer.] Waste grounds, St. Thomas.

SIPHONANTHUS INDICUS L. [*Clerodendron Siphonanthus* R. Br.] Woods near Grove Place and at Crequis, St. Croix. Apparently naturalized. Planted for ornament.

AVICENNIA NITIDA Jacq. [*A. tomentosa* Jacq.; *A. officinalis nitida* Kuntze.] Coastal swamps and lagoons, St. Thomas; St. Jan; St. Croix.

PETRAEA VOLUBILIS Jacq. Planted for ornament.

HOLMSKOLDIA SANGUINEA Retz. Planted for ornament.

VERBENA ICHAMAEDRIFOLIA Juss. Planted for ornament.

## LAMIACEAE

LEONOTIS NEPETIFOLIA (L.) R. Br. [*Phlomis nepetifolia* L.] Waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

LEONURUS SIBIRICUS L. Waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

MOLUCCELLA LAEVIS L. St. Croix (according to West).

LEUCAS MARTINICENSIS (Jacq.) R. Br. [*Clinopodium martinicense* Jacq.] Waste and cultivated grounds, St. Croix.

SALVIA THOMASIANA Urban. [*S. tenella* of Schlechtendal and of Eggers.] St. Thomas. Endemic. Known only from a specimen collected long ago by Ehrenberg.

SALVIA OCCIDENTALIS Sw. [*S. occidentalis bicolor* Kuntze.] Banks, fields and thickets, St. Thomas; St. Jan; St. Croix.

SALVIA SEROTINA L. [*S. dominica* Sw.; *S. micrantha* Vahl.] Banks, fields and hillsides, St. Thomas; St. Jan; St. Croix.

SALVIA COCCINEA B. Juss. [*S. coccinea ciliata* Griseb.; *S. coccinea pseudococcinea* Kuntze.] Hillsides, waste and cultivated grounds, St. Thomas; St. Croix; St. Jan.

MENTHA AQUATICA L. Naturalized along rivulets, Caledonia, St. Croix, not seen flowering (according to Eggers). Perhaps, if the flowers were known, referable to some other species.

HYPTIS CAPITATA Jacq. [*Mesosphaerum capitatum* Kuntze.] Moist grounds, St. Thomas; St. Jan; St. Croix.

HYPTIS SUAVEOLENS (L.) Poir. [*Ballota suaveolens* L.; *Mesosphaerum suaveolens* Kuntze.] Thickets, waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

HYPTIS PECTINATA (L.) Poir. [*Nepeta pectinata* L.; *Mesosphaerum pectinatum* Kuntze.] Waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

HYPTIS VERTICILLATA Jacq. [*Mesosphaerum verticillatum* Kuntze.] St. Thomas (according to Bentham and to Grisebach).

COLEUS AMBOINICUS Lour. Banks and hillsides, naturalized, St. Thomas; St. Jan (according to Eggers); St. Croix.

OCIMUM MICRANTHUM Willd. Banks, fields and hillsides; St. Thomas; St. Jan; St. Croix.

OCIMUM BASILICUM L. Grown as a garden herb.

ROSMARINUS OFFICINALIS L. Grown as a garden herb.

THYMUS VULGARIS L. Grown as a garden herb.

ORIGANUM MAJORANA L. Grown as a garden herb.

## SOLANACEAE

PHYSALIS ANGULATA L. [*P. ramosissima* Mill.; *P. Linkiana* Griseb., not Nees.] Fields, banks, waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

PHYSALIS PUBESCENS L. [*P. angulata dubia* Kuntze.] Dry soil, waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

PHYSALIS TURBINATA Medic. Dry soil, St. Jan; St. Croix.

PHYSALIS EGGERSII O. E. Schulz. Water Island, St. Thomas. Endemic. A species known only from the type specimen. We searched Water Island for it in 1913, but could find nothing answering the description.

PHYSALIS PERUVIANA L., recorded by Eggers as found in fields at Rapoon, St. Thomas, prior to 1879, was, apparently, erroneously determined (see Schulz in Urban, Symb. Ant. 6: 149).

CAPSICUM FRUTESCENS L. Roadsides and woods, St. Thomas; St. Jan; St. Croix.

CAPSICUM BACCATUM L. [*Capsicum annuum baccatum* Kuntze.] Thickets, banks and woods, St. Thomas; St. Jan; St. Croix (according to Eggers).

CAPSICUM ANNUUM L. Cultivated for food.

CAPSICUM DULCE Dunal. Cultivated for food.

SOLANUM LANCEIFOLIUM Jacq. King's Hill, St. Jan.

SOLANUM JAMAICENSE Mill. St. Thomas, collected by Richard (according to Poiret).

SOLANUM NIGRUM L. [*S. americanum* Mill.; *S. nigrum nodiflorum* A. Gray; *S. nodiflorum* Dunal, not Jacq.] Thickets, waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

SOLANUM SEAFORTHIANUM Andr. Spontaneous after cultivation, St. Thomas; St. Croix. Planted for ornament.

SOLANUM VERBASCIFOLIUM L. Hillsides and thickets, St. Thomas; St. Jan; St. Croix.

SOLANUM CONOCARPUM L. C. Rich. Coral Bay, St. Jan. Endemic.

SOLANUM MUCRONATUM O. E. Schulz. St. Thomas; St. Jan; otherwise known only from Porto Rico.

SOLANUM MAMMOSUM L. Waste grounds, St. Croix.

SOLANUM PERSICIFOLIUM Dunal. [*S. persicifolium Belloi* O. E. Schulz; *S. persicifolium parvifolium* (Vahl) O. E. Schulz.] Hillsides and thickets, St. Thomas; St. Jan; St. Croix.

SOLANUM RACEMOSUM L. [*S. ignaeum* L.; *S. bahamense* of Eggers.] Thickets, St. Thomas; St. Jan; St. Croix.

SOLANUM TORVUM Sw. Hillsides, woods and waste grounds, St. Thomas; St. Jan; St. Croix.

SOLANUM POLYGAMUM Vahl. [*S. inclusum* and *S. inclusum albiflorum* of Eggers; *S. polygamum thomae* Kuntze; *S. hirtum* of Borgesen & Paulsen.] Thickets, St. Thomas; St. Jan; St. Croix.

SOLANUM ACULEATISSIMUM Jacq. Naturalized by mules from Montevideo at Frederiksted, St. Croix (according to Eggers).

SOLANUM TUBEROSUM L. Cultivated for food.

SOLANUM MELONGENA L. [*S. insanum* L.] Cultivated for food.

SOLANUM MACROCARPUM L. Cultivated on St. Croix (according to Schulz).

SOLANUM PSEUDOCAPSICUM L. Cultivated for its fruit.

LYCOPERSICUM LYCOPERSICUM (L.) Karst. [*Solanum Lycopersicum* L.; *Lycopersicum esculentum* Mill.; *L. cerasiforme* Dunal.] Spontaneous after cultivation for food, St. Thomas; St. Jan; St. Croix.

DATURA STRAMONIUM L. [*Datura Tatula* L.] Waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

DATURA METEL L. Waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

DATURA FASTUOSA L. Spontaneous after cultivation, St. Thomas; St. Jan; St. Croix.

DATURA SUAVEOLENS H. & B. Cultivated for ornament.

CESTRUM NOCTURNUM L. Forests, Rogiers and Joshee Gut, St. Jan (according to Eggers). Planted on St. Croix.

CESTRUM LAURIFOLIUM L'Her. [*C. diurnum* of West and of Eggers; *C. laurifolium neglectum* Kuntze.] Forests and thickets, St. Thomas; St. Jan; St. Croix.

CESTRUM ALTERNIFOLIUM (Jacq.) O. E. Schulz. [*Ixora alternifolia* Jacq.; *Cestrum vespertinum* L.] St. Thomas (according to O. E. Schulz).

NICOTIANA TABACUM L. Spontaneous after cultivation, St. Thomas; St. Jan; St. Croix.

Brunfelsia americana L. [*B. americana pubescens* Griseb.] Thickets and hillsides, St. Thomas; St. Jan; St. Croix. Sometimes planted for ornament.

Petunias are planted in gardens.

## SCROPHULARIACEAE

Mecardonia procumbens (Mill.) Small. [*Erinus procumbens* Mill.; *Herpestis chamaedryoides* H.B.K.; *Lindernia dianthera* Sw.; *Monniera dianthera* Millsp.] Wet grounds, St. Croix.

Herpestis stricta Schrad., accredited to St. Thomas by Bentham, according to Eggers, is probably an error in record.

Bramia Monniera (L.) Drake. [*Gratiola Monniera* L.; *Herpestis Monniera* H.B.K.; *Monniera Monniera* Britton; *M. calycina* Kuntze.] Wet sandy or muddy situations, St. Thomas; St. Jan; St. Croix.

Capraria biflora L. [*C. biflora pilosa* of Eggers.] Fields, banks, waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

Vandellia diffusa L. St. Croix (according to Eggers).

Scoparia dulcis L. [*Capraria dulcis* Kuntze.] Wet or moist situations and in cultivated grounds, St. Thomas; St. Jan; St. Croix.

Russellia equisetiformis Schl. & Cham. [*R. juncea* Zucc.] Cultivated for ornament.

Maurandya Barclayana Lindl. Cultivated for ornament.

## BIGNONIACEAE

Macrodiscus lactiflorus (Vahl) Bureau. [*Bignonia lactiflora* Vahl; *Distictis lactiflora* DC.] Thickets and roadsides, St. Croix. Cultivated on St. Thomas (according to Eggers).

Cydista aequinoctialis (L.) Miers. [*Bignonia aequinoctialis* L.; *B. spectabilis* Vahl.] Forests and thickets, St. Thomas; St. Jan; St. Croix.

Batocydia Unguis (L.) Mart. [*Bignonia Unguis* L.] Forests, St. Thomas; St. Jan; St. Croix.

Macrocatalfa longissima (Jacq.) Britton. St. Thomas (according to Grisebach). The record is probably erroneous.

Tabebuia heterophylla (DC.) Britton. [*Raputia* (?) *heterophylla* DC.; *Tecoma Berterii* of Eggers, not DC.; *Tecoma triphylla* of Kuntze; *Tecoma Leucoxylon* Mart.; *Tecoma pentaphylla Leucoxylon* Kuntze.] Dry thickets, especially near the coasts, St. Thomas; St. Jan.

Tabebuia pallida Miers. [*Bignonia pentaphylla* L.; *Tecoma pentaphylla* Juss., not *Tabebuia pentaphylla* Hemsl.; *T. Leucoxylon* of Eggers.] Forests and hills and much planted for shade, St. Thomas; St. Jan; St. Croix.

TECOMA STANS (L.) Juss. [*Bignonia stans* L.; *Stenolobium stans* Seem.; *Gelseminum stans* Kuntze.] Thickets and hillsides, St. Thomas; St. Jan; St. Croix. Sometimes planted for ornament.

TECOMARIA CAPENSIS (Thunb.) Spach. [*Bignonia capensis* Thunb.; *Tecoma capensis* Lindl.] Roadsides, St. Thomas. Planted for ornament, St. Thomas; St. Croix.

ENALLAGMA LATIFOLIA (Mill.) Small. [*Crescentia latifolia* Mill.; *Crescentia cucurbitina* L.; *C. cucurbitina heterophylla* Kuntze; *E. cucurbitina* Baill.] Forests near rivulets, St. Thomas; St. Jan; St. Croix.

CRESCENTIA CUJETE L. Forests, hillsides and much planted for its fruit, St. Thomas; St. Jan; St. Croix.

CRESCENTIA LINEARIFOLIA Miers. Collected by Oersted on St. Thomas (according to Miers); coastal hill, Lamosure, St. Jan.

## PEDALIACEAE

SESAMUM ORIENTALE L. [*S. indicum* L.] Spontaneous after cultivation, St. Thomas. Cultivated for its seeds.

## MARTYNIACEAE

MARTYNIA ANNUA L. [*M. diandra* Glox.] Waste and cultivated grounds, St. Thomas; St. Croix.

## ACANTHACEAE

THUNBERGIA FRAGRANS Roxb. [*T. volubilis* Pers.] Hedges and thickets and along ditches, St. Thomas; St. Jan; St. Croix.

THUNBERGIA ALATA Bojer. Banks and waste grounds, St. Thomas. St. Jan; St. Croix. Planted for ornament.

BLECHUM BROWNEI Juss. [*B. Brownei subcordatum* and (?) *laxum* Kuntze.] Fields, banks, woods and thickets, St. Thomas; St. Jan; St. Croix.

RUELLIA TUBEROSA L. [*R. clandestina* L.] Grassy situations, St. Thomas; St. Jan; St. Croix.

RUELLIA COCCINEA (L.) Vahl. [*Barleria coccinea* L.; *Stemonacanthus coccineus* Griseb.] Thickets, St. Thomas; St. Jan; St. Croix.

RUELLIA STREPENS L., recorded by de Candolle as found on St. Croix by Isert, must be an error in locality; the specimen is preserved in the Willdenow herbarium.

GERARDIA TUBEROSA L. [*Stenandrium tuberosum* Urban; *S. rupestre* Nees.] Rocky woods and thickets, St. Thomas; St. Jan.

ANTHACANTHUS SPINOSUS (Jacq.) Nees. [*Justicia spinosa* Jacq.; *A. microphyllus* and *A. jamaicensis* of Eggers; *Jasminum coeruleum*

Kuntze.] Woods, hillsides and thickets, St. Thomas; St. Jan; St. Croix.

Anthacanthus acicularis (Sw.) Nees, attributed by West and by Lindau to St. Croix, is known to me only from Jamaica. [*Justicia acicularis* Sw.]

Odontonema nitidum (Jacq.) Kuntze. [*Justicia nitida* Jacq.; *Thyrsacanthus nitidus* Nees.] St. Thomas and St. Croix, at least formerly.

Drejerella mirabiloides (Lam.) Lindau. [*Justicia mirabiloides* Lam.; *Beleperone nemorosa* of Eggers.] Shaded situations, St. Thomas; St. Jan; St. Croix.

Diapedium assurgens (L.) Kuntze. [*Justicia assurgens* L.; *Dicliptera assurgens* Juss.] Banks, thickets and waste grounds, St. Thomas; St. Jan; St. Croix.

Justicia periplocifolia Jacq. [*J. reflexiflora* Vahl and var. *glandulosa* Eggers; *Ecbolium reflexiflorum* Kuntze.] Thickets, St. Thomas; St. Jan; St. Croix.

Justicia pectoralis Jacq. [*Dianthera pectoralis* Gmelin.] Waste and cultivated moist grounds, St. Thomas; St. Jan (according to Eggers); St. Croix.

Justicia sessilis Jacq. [*J. pauciflora* Vahl; *Dianthera sessilis* Gmelin; *Siphonoglossa sessilis* Oerst.] Thickets and hillsides, St. Thomas; St. Jan; St. Croix.

Justicia carthaginensis Jacq. Woodlands, hillsides and waste grounds, St. Thomas; St. Croix.

Justicia secunda Vahl. Thickets, St. Croix (according to Lindau).

Barleria lupulina Lindl. Waste grounds, St. Thomas; St. Jan.

Barleria hirsuta Jacq., recorded from St. Thomas by West, is a species unknown to modern botanists except from description and the published illustrations of Jacquin (Obs. 2: *pl. 32*; Icon. Pict. *pl. 172*); it has been referred to *Duggena spicata* of the Rubiaceae, but the description of its flowers does not apply to that plant.

Crossandra infundibuliformis (L.) Nees. Cultivated for ornament.

Graptophyllum pictum (L.) Griff. [*G. hortense* Nees.] Cultivated for ornament.

Pseuderanthemum bicolor (Schrank) Radlk. [*Justicia bicolor* Sims.] Cultivated for ornament.

Eranthemum nervosum R. Br. Cultivated for ornament.

Pachystachys coccinea Nees. Cultivated for ornament.

## MYOPORACEAE

Bontia daphnoides L. Coastal thickets, St. Thomas; St. Jan; St. Croix at Turner's Hole (according to Eggers).

## PLANTAGINACEAE

Plantago major L. [*P. major tropica* Griseb.] Waste grounds, St. Thomas; St. Croix.

## RUBIACEAE

Oldenlandia corymbosa L. Waste places, Government House yard, St. Croix (according to Eggers).

Oldenlandia callitrichoides Griseb. Gregarious among stones, Government House, St. Croix (according to Eggers).

Rondeletia pilosa Sw. [*R. triflora* Vahl.] Thickets, St. Thomas; St. Jan; near Cave Bay, St. Croix (according to Eggers).

Exostema caribaeum (Jacq.) R. & S. [*Cinchona caribaea* Jacq.] Thickets and hillsides, St. Thomas; St. Jan; St. Croix.

Duggena spicata (Lam.) Standley. [*Lygistum spicatum* Lam.; *Gonzalia spicata* DC.; *Gonzalagunia spicata* Maza.] Grassy situations on high hills, St. Thomas; St. Jan.

Randia formosa (Jacq.) K. Schum. [*Mussaenda formosa* Jacq.; *Gardenia armata* Sw.; *Randia Mussaenda* DC.] Roadsides, St. Croix. Planted for ornament.

Randia aculeata L. [*R. latifolia* Lam.; *Gardenia Randia* Sw.; *R. aculeata mitis* of Eggers.] Thickets, woods and hillsides, St. Thomas; St. Jan; St. Croix.

Genipa americana L. Forests on the higher hills, St. Thomas; St. Jan.

Hamelia patens Jacq. Valleys and hillsides, St. Croix; St. Thomas (according to Eggers).

Hamelia axillaris Sw. [*H. lutea* Rohr.] Forests and wet thickets, St. Thomas; St. Croix.

Catesbaea melanocarpa Krug & Urban. [*C. parviflora* of Eggers, not Sw.] Thickets, Fair Plain, St. Croix (according to Eggers).

Guettarda scabra (L.) Lam. [*Matthiola scabra* L.; *G. rugosa* Sw.] Woods and thickets, St. Thomas; St. Jan; St. Croix.

Guettarda parviflora Vahl. [*G. parvifolia* Sw.] Thickets, woods and hillsides, St. Thomas; St. Jan; St. Croix.

Guettarda elliptica Sw. Hillside near Charlotte Amalia, St. Thomas.

Stenostomum lucidum (Sw.) Gaertn. f. [*Laugeria lucida* Sw.; *Antirrhoea lucida* Hook.] Forests, St. Thomas; St. Croix.

ERITHALIS FRUTICOSA L. [*E. odorifera* Jacq.] Thickets along the coast, St. Thomas; St. Jan; St. Croix.

CHIOCOCCA ALBA (L.) Hitchc. [*Lonicera alba* L.; *C. racemosa* L.] Woods and thickets, St. Thomas; St. Jan; St. Croix.

CHIONE VENOSA (Sw.) Urban. [*Jacquinia venosa* Sw.; *Chione glabra* DC.] In forests, rare, not seen flowering, Fair Plain, St. Croix and Soldier Bay, St. Thomas (according to Eggers). Found on Tortola, according to A. Richard.

SCOLOSANTHUS VERSICOLOR Vahl. Thickets, St. Thomas; St. Jan; St. Croix. Known otherwise only from Porto Rico and Vieques.

COFFEA ARABICA L. [*C. liberica* of Millspaugh.] Spontaneous after cultivation, St. Thomas; St. Jan; St. Croix. Cultivated for coffee.

IXORA FERREA (Jacq.) Benth. [*Sideroxyloides ferreum* Jacq.] Forests and rocky hill-tops; St. Thomas; St. Jan.

IXORA STRICTA Roxb. Planted for ornament.

IXORA BANDHUCA Roxb. Planted for ornament.

PSYCHOTRIA PINNULARIS Sessé & Moç. [*P. horizontalis* Griseb. and of Eggers and of Millspaugh, not Sw.] Thickets, St. Thomas; St. Jan; St. Croix.

PSYCHOTRIA UNDATA Jacq. [*P. glabrata* of Eggers.] Thickets, St. Thomas; St. Jan; St. Croix.

PSYCHOTRIA BROWNEI Spreng. [*C. asiatica* of West; *C. tenuifolia* of Millspaugh.] Woods and thickets, St. Thomas; St. Jan; St. Croix.

PSYCHOTRIA TENUIFOLIA Sw. Thickets, Crown, St. Thomas (according to Eggers and cited also by Urban); St. Croix (according to West).

PSYCHOTRIA PUBESCENS Sw. St. Thomas (according to Urban).

PALICOUREA DOMINGENSIS (Jacq.) DC. [*Psychotria domingensis* Jacq.; *P. Pavetta* Sw.; *Palicourea Pavetta* DC.; *P. Pavetta rosea* Eggers.] Forests and thickets, St. Thomas; St. Jan; St. Croix.

GEOPHILA HERBACEA (Jacq.) K. Schum. [*Psychotria herbacea* Jacq.; *G. reniformis* C. & S.] In dense woods, Signal Hill and St. Peter, St. Thomas (according to Eggers); wooded hill, Bordeaux, St. Jan.

FARAMEA OCCIDENTALIS (L.) A. Rich. [*Ixora occidentalis* L.; *Faramea odoratissima* DC.] Forests and thickets, St. Thomas; St. Jan; St. Croix, at least formerly.

MORINDA CITRIFOLIA L. Roadsides and thickets, St. Thomas; St. Croix.

ERNODEA LITTORALIS Sw. Coastal sands, St. Thomas; St. Jan; St. Croix.

DIODIA RIGIDA C. & S. Dry soil, St. Thomas.

DIODIA MARITIMA Thonn. [*D. radicans* of Borgesen and Paulsen.] Coastal sands, Water Island, St. Thomas.

DIODIA SARMENTOSA Sw. St. Thomas (according to Schlechtendal).

BORRERIA LAEVIS (Lam.) Griseb. [*Spermacoce laevis* Lam.; *Borreria vaginata* Cham. & Schl.] Dry soil, St. Thomas; St. Jan; St. Croix.

BORRERIA OCIMOIDES (Burm. f.) DC. [*Spermacoce ocimoides* Burm. f.; *Borreria parviflora* Meyer.] Banks, fields, waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

BORRERIA VERTICILLATA (L.) Meyer. [*Spermacoce verticillata* L.; *B. stricta* DC., not Meyer.] Grassy places, St. Thomas; St. Croix (according to Eggers).

SPERMACOCE TENUIOR L. [*S. tenuior angustifolia* Eggers.] Banks, fields, waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

GARDENIA JASMINOIDES Ellis. [*G. florida* L.] Planted for ornament.

PORTLANDIA GRANDIFLORA L. Planted for ornament.

VANGUERIA EDULIS Vahl. [*Varanga edulis* Vahl] Cultivated on St. Croix (according to West).

## CAPRIFOLIACEAE

LONICERA JAPONICA Thunb. Planted for ornament.

LONICERA CAPRIFOLIUM L. Cultivated (according to Eggers).

SAMBUCUS NIGRA L. Cultivated (according to Eggers).

## CUCURBITACEAE

MELOTHRIA GUADALUPENSIS (Spreng) Cogn. [*Bryonia guadalupensis* Cogn.; *M. pervaga* Griseb.] Thickets, St. Thomas; St. Jan; St. Croix.

MELOTHRIA FLUMINENSIS Gardn. [*M. pendula* Meyer.] St. Croix (according to West and to Cogniaux).

CORALLOCARPUS EMETOCATHARTICUS (Gros.) Cogn. [*Doyerea emetocathartica* Grosourdy; *Anguria glomerata* Eggers; *Corallocarpus glomeratus* Cogn.] Forests, St. Thomas; St. Croix.

ANGURIA PLUMIERIANA Schl. [*A. trilobata* West and of Eggers.] St. Croix.

MOMORDICA CHARANTIA L. Hedges, fences and waste grounds, St. Thomas; St. Jan; St. Croix.

MOMORDICA BALSAMINA L. Cultivated for its fruit, St. Croix.

LUFFA CYLINDRICA (L.) Roemer. [*Momordica cylindrica* L.; ? *M. operculata* of West.] Spontaneous after cultivation, St. Thomas; St. Croix.

Luffa acutangula (L.) Roxb., accredited to St. Thomas by Cogniaux as collected by Finlay, was really from Trinidad.

Cucumis Anguria L. Fields and banks, St. Thomas; St. Jan; St. Croix.

Cucumis sativus L. Cultivated for its fruit.

Cucumis Melo L. Cultivated for its fruit.

Cucurbita Lagenaria L. [*Lagenaria vulgaris* Ser.; *L. vulgaris viscosa* Eggers; *L. Lagenaria* Cockerell.] Waste grounds, spontaneous after cultivation, St. Thomas; St. Croix. Cultivated for its fruit.

Cucurbita ficifolia Bouché is recorded by Millspaugh as escaped from cultivation on St. Croix.

**Pepo moschata** (Duch.) Britton. [*Cucurbita moschata* Duch.; *C. Pepo* of Eggers.] Spontaneous after cultivation, St. Thomas; St. Croix.

Cayaponia americana (Lam.) Cogn. [*Bryonia americana* Lam.; *B. ficifolia* Vahl; *Trianosperma graciliflora* Griseb.; *T. ficifolia* of Eggers; *Cayaponia graciliflorum* Griseb.] Woods and thickets, St. Thomas; St. Jan; St. Croix.

Sechium edule (Jacq.) Sw. Cultivated for its fruit.

Citrullus Citrullus (L.) Karst. [*C. vulgaris* Schrad.] Cultivated for its fruit.

Coccinia cordifolia (L.) Cogn. [*Cephalandra indica* Naud.] Cultivated; recorded by Eggers as naturalized in shaded valleys, St. Croix.

## LOBELIACEAE

Isotoma longiflora (L.) Presl. [*Lobelia longiflora* L.] Moist banks, fields and hillsides, St. Thomas; St. Jan; St. Croix (according to Eggers).

## GOODENIACEAE

Scaevola Plumierii (L.) Vahl. [*Lobelia Plumierii* L.] Coastal sands, St. Thomas; St. Croix.

## CICHORIACEAE

Sonchus oleraceus L. Waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

Lactuca intybacea Jacq. [*Brachyramphus intybaceus* DC.] Waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

Lactuca sativa L. Cultivated for salad.

## AMBROSIACEAE

Xanthium longirostre Wallr. [*X. orientale* of Schlechtendal: *X. macrocarpum* of Eggers; *X. strumarium* of Millspaugh; *X. echi-*

*natum* of Urban.] Waste and cultivated grounds, St. Thomas; all islands (according to Eggers).

AMBROSIA CUMANENSIS H.B.K. [*A. artemisiaefolia trinitensis* Griseb.] Waste places, St. Croix (according to Eggers).

## CARDUACEAE

STRUCHIUM SPARGANOPHORUM (L.) Kuntze. [*Ethulia sparganophora* L.; *Sparganophorus Vaillantii* Crantz.] Moist grounds, St. Thomas (according to Eggers).

VERNONIA SERICEA L. C. Rich. [*Lepidoploa phyllostachya* Cass.; *Vernonia arborescens Swartziana, Lessingiana* and *divaricata* of Eggers; *V. arborescens* of Schlechtendal and of Millspaugh; *V. phyllostachya* Gleason; *Cacalia arborescens Lessingiana* Kuntze.] Thickets, St. Thomas; St. Jan; St. Croix.

VERNONIA ALBICAULIS Pers. [*V. longifolia* Pers.; *V. Vahliana* Less.; *V. thomae* Benth.; *V. punctata* of Eggers and of Millspaugh; *Cacalia thomae* Kuntze; ? *Conyza fruticosa* of West.] Thickets, St. Thomas; St. Jan; St. Croix.

VERNONIA CINEREA (L.) Less. [*Conyza cinerea* L.] Waste and cultivated grounds, St. Thomas; St. Croix.

PIPTOCOMA RUFESCENS Cass. Thickets, Water Island, St. Thomas; St. Jan.

ELEPHANTOPUS MOLLIS H.B.K. [*E. tomentosus* of Millspaugh.] Banks, fields and hillsides, St. Thomas; St. Jan; St. Croix.

PSEUDELEPHANTOPUS SPICATUS (Juss.) Rohr. [*Elephantopus spicatus* Juss.; *Distreptus spicatus* Rohr.] Banks, fields, hillsides and cultivated grounds, St. Thomas; St. Jan; St. Croix.

AGERATUM CONYZOIDES L. [*Carelia conyzoides robusta* Kuntze.] Banks, fields and roadsides, St. Thomas; St. Jan; St. Croix.

EUPATORIUM MACROPHYLLUM L. [*Hebeclinium macrophyllum* DC.] Forests, St. Thomas; St. Croix (according to West and to Eggers).

EUPATORIUM ODORATUM L. [*E. conyzoides* Vahl.] Banks, hillsides and thickets, St. Thomas; St. Jan; St. Croix.

EUPATORIUM CUNEIFOLIUM Willd., cited by Eggers from DeCandolle (Prodr. 5: 177) as from St. Thomas, was not from our island St. Thomas.

EUPATORIUM ATRIPLICIFOLIUM Lam. [*E. repandum* Willd.; *Erigeron atriplicifolium* of Millspaugh.] Hillsides and coastal thickets, St. Thomas; St. Jan; St. Croix.

EUPATORIUM SINUATUM Lam. [*E. canescens* Vahl.] Rocky thickets, St. Thomas (according to DeCandolle); rocky hillsides, St. Jan; St. Croix.

EUPATORIUM TRIPLINERVE Vahl. [*E. Ayapana* Vent.] Cultivated on St. Croix.

EUPATORIUM CAPILLIFOLIUM (Lam.) Small. [*E. foeniculaceum* Willd.] Cultivated on St. Croix (according to Millspaugh).

MIKANIA CORDIFOLIA (L. f.) Willd. [*Cacalia cordifolia* L. f.; ? *Eupatorium denticulatum* of Schlechtendal; *Mikania gonoclada* DC.; *Willughbaea cordifolia* Kuntze; *W. gonoclada* Millsp.] Thickets, St. Thomas; St. Jan; St. Croix.

ERIGERON CUNEIFOLIUS DC. Grassy places and banks on the higher hills, St. Thomas; St. Jan.

ERIGERON SPATHULATUS Vahl. Grassy situations, St. Thomas; St. Jan; St. Croix.

LEPTILON PUSILLUM (Nutt.) Britton. [*Erigeron pusillum* Nutt.; *Erigeron canadense* of Schlechtendal and of Eggers; *Leptilon canadense* of Millspaugh.] Grassy places, waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

LEPTILON LINIFOLIUM (Willd.) Small. [*Erigeron linifolium* Willd.; *Conyza ambigua* DC.] Waste grounds, St. Thomas.

PLUCHEA PURPURASCENS (Sw.) DC. [*Conyza purpurascens* Sw.; *P. camphorata* of Millspaugh.] Wet grounds, St. Thomas; St. Croix.

PLUCHEA ODORATA (L.) Cass. [*Conyza odorata* L.; *C. carolinensis* Jacq.; *P. odorata normalis* Kuntze.] Thickets and hillsides and in cultivated grounds, St. Thomas; St. Jan; St. Croix.

BACCHARIS DIOICA Vahl. [*B. Vahlii* DC.] Coastal rocks, St. Croix.

EGLETES PROSTRATA (Sw.) Kuntze. [*Matricaria prostrata* Sw.; *Pyrethrum simplicifolium* Willd.; *E. domingensis* Cass.] Sandy shores, St. Thomas.

PTEROCAULON VIRGATUM (L.) DC. [*Gnaphalium virgatum* L.; *Conyza virgata* L.; *Pluchea virgata* Schl.] Hillsides and banks, St. Thomas; St. Jan; St. Croix.

NOCCA MOLLIS (Cav.) Jacq. [*Lagascea mollis* Jacq.] Waste grounds, St. Thomas.

MELAMPODIUM DIVARICATUM (L. C. Rich.) DC. [*Dysodium divaricatum* L. C. Rich.; *M. paludosum* H.B.K.] Ditches, St. Croix.

PARTHENIUM HYSTEROPHORUS L. Waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

CRASSINA MULTIFLORA (L.) Kuntze. [*Zinnia multiflora* L.] Roadsides and banks, St. Thomas; St. Jan.

CRASSINA ELEGANS (Jacq.) Kuntze. Grown in flower gardens.

VERBESINA ALBA L. [*Eclipta alba* Hassk.; *E. punctata* L.; *E. erecta* L.] Wet grounds, St. Thomas; St. Jan; St. Croix.

ACANTHOSPERMUM HISPIDUM DC. [*A. humile* of Eggers.] Waste and cultivated grounds, St. Thomas; St. Croix.

Borrichia arborescens (L.) DC. [*Buphthalmum arborescens* L.; *B. argentea* DC.] Coastal rocks and sands, St. Thomas; St. Croix.

Wedelia trilobata (L.) Hitchc. [*Silphium trilobatum* L.; *W. carnosa* L. C. Rich.] Moist grounds, St. Thomas; St. Croix.

Wedelia calycina L. C. Rich. [*Buphthalmum helianthoides* of West.] Thickets, St. Thomas; St. Croix.

Wedelia parviflora L. C. Rich. [*W. buphthalmoides* of Eggers and of Millspaugh; *W. affinis* DC.; *W. acapulcensis* of Schlechtendal; *W. brachycarpa* of Millspaugh, St. Thomas; *Sereneum frutescens* of Kuntze.] Dry hills and thickets, St. Thomas; St. Jan.

Wedelia cruciana L. C. Rich. [*W. buphthalmoides* of Millspaugh.] Dry rocky soil, St. Croix. Endemic.

Eleutheranthera ruderalis (Sw.) Sch. Bip. [*Melampodium ruderale* Sw.; *Ogiera ruderalis* Griseb.; *Wedelia discoidea* Less.] Banks, fields and waste grounds, St. Thomas; St. Jan; St. Croix.

Melanthera canescens (Kuntze) O. E. Schulz. [*Amellus asper canescens* Kuntze; *M. Linnaei* of Schlechtendal; *M. deltoidea* of Eggers.] Hillsides and thickets, St. Thomas.

Tepion alatum (L.) Britton. [*Verbesina alata* L.] Waste and cultivated ground, St. Thomas; St. Croix.

Sclerocarpus africanus Jacq. Waste grounds, St. Thomas.

Synedrella nodiflora (L.) Gaertn. [*Verbesina nodiflora* L.; *Ucacou nodiflorum* Hitchc.] Waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

Bidens pilosa L. [*Coreopsis leucantha* L.; *B. leucantha* Willd.; *B. pilosa dubia* O. E. Schulz; ? *B. pilosa subbiternata* Kuntze.] Waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

Bidens cynapiifolia H.B.K. [*B. bipinnata* of West, of Eggers and of Millspaugh.] Waste and cultivated grounds, St. Thomas; St. Jan; St. Croix.

Cosmos caudatus H.B.K. [*Bidens Berteriana* Spreng.] Grassy fields, banks, and in waste grounds, St. Thomas; St. Jan; St. Croix.

Porophyllum Porophyllum (L.) Kuntze. [*Cacalia Porophyllum* L.; *Porophyllum ellipticum* Cass.] Waste grounds, St. Thomas.

Pectis humifusa Sw. [*P. serpyllifolia* Pers.] Stony banks, fields, and hillsides, St. Thomas; St. Jan; St. Croix.

Pectis linifolia L. [*Pectis punctata* Jacq.; *Pectidium punctatum* Less.] Rocky hillsides, banks and thickets, St. Thomas; St. Jan; St. Croix.

Pectis febrifuga H. van Hall. [*P. Swartziana* of Borgesen and Paulsen.] Grassy places, St. Thomas; St. Croix.

Neurolaena lobata (L.) R. Br. [*Conyza lobata* L.] Woodlands, St. Thomas.

Erechthites hieracifolia (L.) Raf. [*Senecio hieracifolius* L.; *E. praealta* Raf.; *E. hieracifolia cacalioides* of Eggers and of Kuntze.] Banks, fields, waste and cultivated grounds, St. Thomas; St. Croix.

Emilia sonchifolia (L.) DC. [*Cacalia sonchifolia* L.; *E. sonchifolia sagittata* of Kuntze.] Banks, fields, waste and cultivated grounds, St. Thomas; St. Croix; St. Jan.

Emilia sagittata (Vahl) DC. Grown in flower gardens.

Chaptalia nutans (L.) Polak. [*Tussilago nutans* L.; *Leria nutans* DC.] Woods and thickets, St. Thomas; St. Jan; St. Croix.

Chrysoganum dichotomum Vahl, of St. Croix, is unknown to me; it is certainly not a *Chrysoganum.*

Helianthus annuus L. Grown in gardens.

Chrysanthemum indicum L. [*Pyrethrum indicum* Cass.] Grown in gardens.

Aster chinensis L. Grown in gardens.

Tagetes patula L. Grown in gardens.

Tithonia tagetiflora Desf. [*T. speciosa* Hook.] Grown in gardens.

Georgina variabilis Willd. Grown in gardens (according to Eggers).

Tarchonanthus camphoratus L. Cultivated on St. Croix (according to Eggers).

### PINACEAE

Thuja orientalis L. Planted for ornament.

Juniperus bermudiana L. Planted on St. Croix (according to West).

### CYCADACEAE

Cycas revoluta Thunb. Planted for ornament.

## PTERIDOPHYTA

### CYATHEACEAE

Cyathea arborea (L.) J. E. Smith. [*Polypodium arboreum* L.; ? *C. Serra* of Kuhn.] Forests, high hills, St. Thomas.

### POLYPODIACEAE

Dryopteris patens (Sw.) Kuntze. [*Polypodium patens* Sw.; *Aspidium patens* Sw.] Forests, high hills of St. Thomas; St. Croix.

Dryopteris oligophylla Maxon. [*Polypodium invisum* Sw.] St. Thomas (according to Christensen).

Dryopteris incisa (Sw.) Kuntze. [*Polypodium incisum* Sw.] St. Croix (West, according to Eggers).

Dryopteris Sprengelii (Kaulf.) Kuntze. [*Dryoteris Balbisii* Urban; *Polypodium Balbisii* Spreng.] St. Thomas (according to Kuhn).

Dryopteris serra (Sw.) Kuntze. [*Polypodium serra* Sw.; *Tectaria incisa* Cav.; *Dryopteris serra incisa* Kuhn.] St. Thomas (according to Kuhn).

Dryopteris mollis (Jacq.) Hieron. [*Aspidium molle* Sw.] Forests, Signal Hill, St. Thomas; St. Jan; St. Croix (according to Millspaugh).

Dryopteris tetragona (Sw.) Urban. [*Polypodium tetragonum* Sw.] Forests, St. Thomas; St. Jan; St. Croix.

Dryopteris Poiteana (Bory) Urban. ]*Polypodium crenatum* Sw., not Forst; *Lastrea Poiteana* Bory.] St. Thomas and St. Croix (according to Eggers); St. Croix (according to West).

Cyclopeltis semicordata (Sw.) J. Smith. [*Polypodium semicordatum* Sw.; *Aspidium semicordatum* Sw.] Shaded localities, Virgin Islands (according to Eggers).

Gymnopteris nicotianifolia (Sw.) Presl. [*Acrostichum nicotianum* Sw.], attributed by Swartz to St. Thomas, was probably from Porto Rico.

Nephrolepis exaltata (L.) Schott. [*Polypodium exaltatum* L.] Forests, St. Thomas; St. Croix. Cultivated on St. Croix (according to Millspaugh).

Nephrolepis rivularis (Vahl) Mett. [*Polypodium rivulare* Vahl.] St. Thomas (according to Kuhn).

Nephrolepis biserrata (Sw.) Schott. [*Aspidium biserratum* Sw.; *Aspidium acutum* Schk.; *Nephrolepis acuta* Presl.; *Aspidium punctulatum* Sw.] Forests, St. Thomas (according to Eggers); St. Croix.

Odontosoria aculeata (L.) J. Smith. [*Adiantum aculeatum* L.; *Davallia aculeata* J. E. Smith.] Pastures on high hills, St. Thomas.

Odontosoria clavata (L.) J. Smith, is doubtfully attributed to St. Thomas by Fée.

Asplenium serratum L. Forests, Signal Hill, St. Thomas.

Asplenium pumilum Sw. Forests and wet banks, St. Thomas; St. Jan.

Asplenium abscissum Willd. [*A. firmum* Kunze.] St. Thomas (according to Grisebach).

Blechnum occidentale L. Banks, fields and forests, St. Thomas; St. Jan; St. Croix.

Pityogramma sulphurea (Sw.) Maxon. [*Gymnogramme sulphurea* Desv.]. Cultivated in gardens.

Pityogramma calomelana (L.) Link. [*Acrostichum calomelanos* L.; *Gymnogramme calomelanos* Kaulf.; *G. calomelanos pumila* Eggers.] Banks, hills, walls and thickets, St. Thomas; St. Jan; St. Croix.

HEMIONITIS PALMATA L. Forests, wet banks and rocky thickets, St. Thomas; St. Jan; St. Croix.

DORYOPTERIS PEDATA (L.) Fée. [*Pteris pedata* L.] Forests and shaded banks, St. Thomas; St. Jan.

CHEILANTHES MICROPHYLLA Sw. [*Adiantum microphyllum* Sw.] Rocky slopes, St. Thomas; St. Croix (according to West and to Eggers).

ADIANTUM VILLOSUM L. Forests, St. Thomas; St. Croix.

ADIANTUM LATIFOLIUM Lam. [*A. denticulatum* Sw.; *A. intermedium* of Eggers; *A. obliquum intermedium* of Millspaugh.] Shaded banks, hills of St. Thomas.

ADIANTUM CRISTATUM L. [? *A. microphyllum* of Eggers.] Hillsides, St. Thomas.

ADIANTUM TENERUM Sw. Shaded banks and ravines on high hills, St. Thomas; St. Jan (according to Eggers); St. Croix.

ADIANTUM FRAGILE Sw. Thickets and walls, St. Thomas; St. Jan; St. Croix.

ADIANTUM FARLEYENSE Moore. Cultivated on St. Croix (*A. foliosum* of Millspaugh).

PYCNODORIA LONGIFOLIA (L.) Britton. [*Pteris longifolia* L.] Along rivulets in forests, St. Croix; in a water spout, St. Thomas.

PTERIS BIAURITA L. St. Thomas (according to Kuhn).

ANTROPHYUM LINEATUM (Sw.) Kaulf. [*Hemionitis lineata* Sw.] Forest, St. Peter, St. Thomas (according to Eggers).

PALTONIUM LANCEOLATUM (L.) Presl. [*Pteris lanceolata* L.; *Taenitis lanceolata* R. Br.; *Heteropteris lanceolata* Fée.] On rocks and trees in forests, St. Thomas; all islands (according to Eggers).

POLYPODIUM POLYPODIOIDES (L.) Hitchc. [*Acrostichum polypodioides* L.; *P. incanum* Sw.] On trees, St. Thomas; St. Jan; St. Croix (according to Eggers).

PHLEBODIUM AUREUM (L.) J. Sm. [*Polypodium aureum* L.] On trees and rocks, St. Thomas; St. Jan; St. Croix.

PHLEBODIUM AREOLATUM (H. & B.). J. Sm. [*Polypodium areolatum* H. & B.] On trees, St. Thomas; St. Jan.

LEPICYSTIS PILOSELLOIDES (L.) Diels. [*Polypodium piloselloides* L.] In forests among rocks, Signal Hill, St. Thomas.

PHYMATODES EXIGUUM (Hew.) Underw. [*Polypodium exiguum* Hew.; *P. serpens* Sw., not Forst.; *P. Swartzii* Baker.] On trees, Bordeaux, St. Jan; St. Croix.

CAMPYLONEURUM PHYLLITIDIS (L.) Presl. [*Polypodium Phyllitidis* L.; *P. Phyllitidis repens* of Eggers.] On rocks and trees in forests, St. Thomas; St. Jan; St. Croix.

CAMPYLONEURUM LATUM Moore. Shaded rocks, Bethania, St. Jan.

ACROSTICHUM AUREUM L. [*Chrysodium vulgare* Fée.] Borders of marshes, St. Thomas; St. Croix.

### OPHIOGLOSSACEAE

OPHIOGLOSSUM RETICULATUM L. Grassy places among rocks, Crown, St. Thomas; shaded bank, Bordeaux, St. Jan.

### LYCOPODIACEAE

LYCOPODIUM CERNUUM L. Among rocks in higher hills, St. Thomas.

### PSILOTACEAE

PSILOTUM NUDUM (L.) Griseb. [*Lycopodium nudum* L.; *P. triquetrum* Sw.] Shaded places among rocks, Signal Hill, St. Thomas; Bordeaux, St. Jan; Crequis, St. Croix.

## BRYOPHYTA

### MUSCI[4]

DICRANELLA LONGIROSTRIS (Schwaegr.) Mitten. [*Trematodon longirostris* Schwaegr.] St. Jan.

LEUCOLOMA SERRULATUM Bridel. [*L. Riedlei* Besch.] On trees in wet woods, St. Thomas.

OCTOBLEPHARUM ALBIDUM (L.) Hedw. [*Bryum albidum* L.] On roots of *Anthurium*, near Caret Bay, St. Thomas; St. Croix.

FISSIDENS KEGELIANUS C. Muell. [*F. palmatus*—of various authors, not Swartz.] On banks, St. Thomas; St. Jan; St. Croix.

FISSIDENS ELEGANS Bridel. On rocks and earth, St. Thomas; St. Jan.

SYRRHOPODON FLAVESCENS C. Muell. On rotten wood, St. Jan.

CALYMPERES RICHARDI C. Muell. [*C. Breutelii* Besch.; *C. hexagonum* Besch.] On rocks and banks, St. Thomas.

HYMENOSTOMUM BREUTELII (C. Muell.) Broth. [*Weisia Breutelii* C. Muell.; *Gymnostomum Breutelii* Br. & Sch.] On banks, St. Thomas; St. Jan; St. Croix.

HYOPHILA TORTULA (Schwaegr.) Hampe. [*Gymnostomum Tortula* Schwaegr.] St. Croix.

BARBULA AGRARIA (Sw.) Hedw. [*Bryum agrarium* Sw.] On rocks, walls and earth, St. Thomas; St. Jan; St. Croix.

BARBULA CRUEGERI Lond. [*Hyophila uliginosa* E. G. Britton.] Bethania, St. Jan.

PHASCUM SESSILE E. G. Britton. On the ground, Cowell Point and Water Island, St. Thomas.

[4] Contributed by Elizabeth G. Britton.

Bryum Cruegeri Hampe. Bed of stream, Tutu, St. Thomas. Sterile.

Philonotis sphaerocarpa (Sw.) Bridel. [*Mnium sphaericarpum* Sw.] Moist banks, high hills of St. Thomas.

Philonotis tenella (C. Muell.) Jaeger. [*Bartramia tenella* C. Muell.] Wet banks, St. Jan.

Pireella cymbifolia (Sull.) Cardot. [*Pilotrichum cymbifolium* Sull.] On trees near Bethania, St. Jan.

Neckera disticha (Sw.) Hedw. [*Fontinalis disticha* Sw.] On trees, rarely on rocks, St. Peter, St. Thomas.

Neckera jamaicensis (Gmel.) E. G. Britton. [*Hypnum jamaicense* Gmel.] On trees, Bethania, St. Jan.

Callicostella Belangeriana (Besch.) Jaeger. [*Hookeria Belangeriana* Besch.] On stones, Bordeaux, St. Jan.

Stereophyllum leucostegum (Bridel) Mitten. [*Leskea leucostega* Bridel.] On wet or shaded rocks, St. Thomas; St. Jan.

Mittenothamnium diminutivum (Hampe) E. G. Britton. [*Hypnum diminutivum* Hampe.] On old wood, Bordeaux, St. Jan.

Taxithelium planum (Bridel) Mitten. [*Hypnum planum* Bridel.] Wet rocks, logs and tree-roots, St. Thomas; St. Jan.

Sematophyllum admistum (Sull.) Mitten. [*Hypnum admistum* Sull.] Shaded banks, stones and dead wood, St. Thomas; St. Jan.

Haplocladium microphyllum (Sw.) Broth. [*Hypnum microphyllum* Sw.] Shaded bank between Pearl and Bonne Resolution, St. Thomas.

Thuidium cymbifolium (Dz. & Mk.) Br. Jav. Shaded banks, St. Thomas.

Dendropogon rufescens Schimp., a Mexican species, has been credited to St. Thomas in Paris, Index, and accepted by Brotherus, but we have seen no specimens.

## HEPATICAE OF ST. CROIX, ST. JAN, ST. THOMAS AND TORTOLA[5]

In the Synopsis Hepaticarum of Gottsche, Lindenberg and Nees von Esenbeck, published in 1844–47, three species of Hepaticae are listed from St. Croix, one from St. Jan, and one from St. Thomas. Another species, although listed from St. Kitts, was based in all probability on material from St. Jan. A seventh species has been listed from St. Jan by Stephani. These seven species, which are the only ones so far reported from the islands under discussion, deserve a few words of comment.

[5] Contributed by Alexander W. Evans, Yale University.

The first species, *Radula pallens* (Sw.) Dumort., is said to have been found "in St. Crucis insula," the record being based on a specimen in the Weber herbarium. This specimen was originally referred to *Jungermannia complanata* L. (*Radula complanata* Dumort.) by Weber,[6] but the later determination is probably correct.

The second species, *Lejeunea Montagnei* Gottsche, was based on material from the Mascarene Islands and is now regarded as a species of *Euosmolejeunea*. A specimen from St. Croix is listed in the Synopsis but is very problematical and would probably now be referred to some other species. Since the specimen in question has not been available for study, and since no later references to it are to be found in the literature, its status must be left in doubt.

The third species, *Lejeunea bethanica* Gottsche, is based on material collected by Breutel and is said to have come from "prope Bethaniam in Insula St. Christopheri." Many years later Stephani,[7] on the basis of a specimen in the Lindenberg herbarium at Vienna, quoted the species from St. Jan, referring it to the subgenus *Cheilo-Lejeunea*. Still later he apparently changed his ideas regarding the habitat of the plant, citing it from St. Kitts and redescribing it under the name *Cheilolejeunea bethanica* Steph.[8] In studying the Lejeuneae in the Lindenberg herbarium, the writer found two specimens labeled *Lejeunea bethanica*, both of which were collected by Breutel at Bethania, St. Jan. One of these is very fragmentary but is apparently referable to *Rectolejeunea phyllobola* (Nees & Mont.) Evans; the other, which is the specimen studied by Stephani, is (in the writer's opinion) referable to *Lejeunea* rather than to *Cheilolejeunea*. The species was originally described from a specimen in the Gottsche herbarium at Berlin, not available at the present time, and there is therefore a possibility that the actual type may have come from St. Kitts. The evidence, however, is against this view, and it seems permissible to assume that the specimen in the Lindenberg herbarium is identical with the type and that it formed a part of the same collection. Unfortunately *L. bethanica* has not again been collected on either St. Jan or St. Kitts.

The fourth species, *Lejeunea epiphyta* Gottsche, was described as "parasitans in *Lej. bethanica* in Insula St. Johannis prope Bethaniam (Breutel, Hb. G.)." This statement affords further proof that *L. bethanica* came from St. Jan. According to Stephani[9] the specimen of *L. epiphyta* in the Lindenberg herbarium should be referred to

[6] Prodr. Hist. Musc. Hepat. 59. 1815.
[7] Hedwigia **29**: 86. 1890.
[8] Sp. Hepat. **5**: 652. 1914.
[9] Hedwigia **29**: 90. 1890.

*Lejeunea myriocarpa* Nees & Mont., now *Cololejeunea myriocarpa* Evans.

The fifth species, *Anthoceros Breutelii* Gottsche, was said to have been collected near Friedensthal, St. Croix. This species, in 1858, was transferred by its author[10] to the genus *Notothylas*, where it is still retained. The following year Milde[11] showed that the type material of the species did not come from St. Croix but from the Corallberg, St. Jan. There is likewise a specimen from St. Jan in the Mitten herbarium, which is presumably a part of the original collection.

The sixth species, *Lejeunea linguaefolia* Tayl., was found "in Insula St. Thomas (Richard in Hb. Hk. a. 1814)." A specimen of this species in the Lindenberg herbarium is referred by Stephani[12] to *Brachiolejeunea corticalis* (Lehm. & Lindenb.) Schiffn., and the writer would make the same disposition of a specimen in the Mitten herbarium.[13] Recently, however, Stephani has apparently thrown doubt on the propriety of this reduction. In the fifth volume of his Species Hepaticarum (1912), on page 35, he includes *L. linguaefolia* among the species of *Ptychocoleus*, citing it as *Pt. linguaefolius* Steph., and adds that he has been unable to see the plant and that his diagnosis is simply a translation of the original description. On page 127, nevertheless, he again quotes *L. linguaefolia* among the synonyms of *B. corticalis*. Since Stephani's original reduction was based on the study of an actual specimen, the writer would regard *Pt. linguaefolius* as nothing more than an unnecessary synonym.

The seventh and last species, *Riccia Breutelii* Hampe, is described as new by Stephani in the first volume of his Species Hepaticarum (1898), on page 17, the habitat being given as "Insulae S'Kitts et S. Juan." Dr. Howe informs the writer that there is some question about the identity of the St. Kitts and St. Jan plants and it is therefore omitted from the following list, pending investigation of authentic material.

In February, 1913, a botanical exploration of the islands was carried on under the auspices of the New York Botanical Garden, the Carnegie Institution of Washington and the United States National Museum.[14] The Hepaticae collected by the various members of this expedition form the basis for the present report. The specimens from St. Thomas, unless otherwise noted, were collected by Mrs. Elizabeth G. Britton and Miss Delia W. Marble, those from St. Jan

[10] Bot. Zeit. **16** (Anhang): 21. 1858.
[11] Bot. Zeit. **17**: 50. 1859.
[12] Hedwigia **29**: 22. 1890.
[13] See Bull. Torrey Club **35**: 164. 1908.
[14] See Britton, N. L., Jour. N. Y. Bot. Gard. **14**: 99. 1913.

and Tortola by N. L. Britton and J. A. Shafer, and those from St. Croix by J. N. Rose. The report records also two specimens collected by C. H. Ostenfeld in 1914, one on St. Thomas and one on St. Jan.

1. Riccia Brittonii M. A. Howe.[15]

St. Thomas: on the ground, Water Island, *N. L. Britton, E. G. Britton & J. A. Shafer 148* (a much larger plant than the original).

2. Plagiochila ludoviciana Sulliv.

St. Jan: on wet rocks, Bethania, *360*. St. Thomas: on rocks, St. Peter, *1453*.

3. Radula pallens (Sw.) Dumort.

St. Croix: without definite locality, collector unknown, cited in the Synopsis Hepaticarum.

4. Cololejeunea myriocarpa (Nees & Mont.) Evans.

*Lejeunea epiphyta* Gottsche.

St. Croix: without definite locality. St. Jan: near Bethania, *J. C. Breutel*. St. Thomas: on rotten wood, near Magin's Bay, *1317*. Tortola: on a rock, Road Town to High Bush, 325 m. alt., *786* (a trace only).

5. Lejeunea bethanica Gottsche.

*Cheilolejeunea bethanica* Steph.

St. Jan: near Bethania, *J. C. Breutel*.

6. Lejeunea glaucescens Gottsche.

St. Thomas: on tree roots, Bonne Resolution, *441*.

7. Lejeunea minutiloba Evans.

St. Thomas: St. Peter, *1251*, *1254*, *1255;* on stones, Crown, *1365* (type).

8. Lejeunea pililoba Spruce.

St. Croix: on bark of a tree, without definite locality. St. Jan: at base of a tree, Rosenberg, 300 m. alt., *306;* on a shaded rock, Bordeaux, 350 m. alt., *571*. St. Thomas: on ridge north of Charlotte Amalia, *406;* Crown, *1365* (a trace only); on rotten wood, St. Peter, *1451*.

9. Microlejeunea laetevirens (Nees & Mont.) Evans.

St. Thomas: on *Anthurium* roots, Pearl to Bonne Resolution, *1340;* on fern roots, St. Peter, *1253;* on mountain behind Charlotte Amalia, *C. H. Ostenfeld 77*. Tortola: on a rock, Roadtown to High Bush, 325 m. alt., *786* (in part).

10. Rectolejeunea phyllobola (Nees & Mont.) Evans.

St. Jan: near Bethania, *J. C. Breutel* (specimen in the Lindenberg

[15] Determined by Marshall A. Howe.

herbarium, labeled *L. bethanica*); on *Clusia* roots, Bethania, *355*. St. Thomas: on roots of royal palm, Tutu, *423*. Tortola: on a rock, Roadtown to High Bush, 325 m. alt., *786* (in part); shaded rocks, High Bush, 375 m. alt., *815*.

11. Euosmolejeunea clausa (Nees & Mont.) Evans.
St. Thomas: shaded bank, Pearl to Bonne Resolution, *1339;* on the ground, St. Peter, *1455*.

12. Euosmolejeunea duriuscula (Nees) Evans.
St. Jan: shaded rocks, Bordeaux, 330 m. alt., *570*. St. Thomas: on rocks, St. Peter, *1452;* on rocks, Crown, *1454*.

13. Euosmolejeunea trifaria (Nees) Schiffn.
St. Thomas: on rocks, St. Peter, *1252;* on a rotten log, Crown, 450 m. alt., *1367*.

14. Taxilejeunea obtusangula (Spruce) Evans.
St. Jan: on a stone, Bordeaux, 400 m. alt., *582*.

15. Mastigolejeunea auriculata (Wils. & Hook.) Schiffn.
St. Jan: on a tree, Bethania to Rosenberg, *243;* on a wet rock, Bethania *356*, *362;* on loose blocks, Little Cruz Bay, *C. H. Ostenfeld 391*. St. Thomas: on a rock, St. Peter, *1256;* on rocks in ravine below Tutu, *1290*.

16. Brachiolejeunea corticalis (Lehm. & Lindenb.) Schiffn.
*Lejeunea linguaefolia* Tayl.
*Ptychocoleus linguaefolius* Steph.
St. Thomas: without definite locality, *L. C. Richard*.

17. Frullania brasiliensis Raddi.
St. Jan: on wet rocks. Bethania, *363* (mostly, specimens without perianths and therefore somewhat doubtful).

18. Frullania Kunzei Lehm. & Lindenb.
St. Jan: on wet rocks, Bethania, *363* (a trace only); on rocks, Bordeaux, 300 m. alt., *550*.

19. Frullania squarrosa (R. Bl. & N.) Dumort.
St. Thomas: on rocks, ridge north of Charlotte Amalia, *407;* on rocks, Bonne Resolution, *440;* on rocks, Magin's Bay to Mafolie, *1313;* on rocks, Pearl to Bonne Resolution, *1338;* on a stone wall, Crown, 450 m. alt., *1364*.

20. Notothylas Breutelii Gottsche.
*Anthoceros Breutelii* Gottsche.
St. Jan: Corallberg, *J. C. Breutel* (type); without definite locality or collector's name (specimen in Mitten herbarium); Bordeaux, *528*. St. Thomas: on damp earth, Nisky, *N. L. Britton, E. G. Britton &*

*D. W. Marble 76;* hills north of Charlotte Amalia, *409;* on the ground, Magin's Bay to Mafolie, *1312.*

21. Anthoceros punctatus L.

St. Thomas: in a mud hole, Crown, 450 m. alt., *1363.*

## REPORT ON THE LICHENS OF ST. THOMAS AND ST. JAN[16]

The following report is based primarily upon a study of 90 numbers of lichens from St. Thomas and St. Jan Islands; from St. Thomas, 82 numbers collected by Dr. N. L. Britton, Mrs. E. G. Britton, and Miss Delia W. Marble, unless otherwise stated; from St. John, 8 numbers collected by Dr. N. L. Britton and Dr. J. A. Shafer. To these have been added a few species recorded by Nylander in Flora (63: 127. 1880) and two endemic species described by Mueller-Argau. Altogether, we have represented 30 genera with 69 species and varieties, of which three species and one variety are here described as new. The discussion of the characteristics of the lichen-flora will be confined to that of St. Thomas.

There is no peculiar element in the lichen-flora of St. Thomas comparable with the gelatinous rock-lichens of Mona Island (see Annals Missouri Bot. Gard. 2: 35. 1915), or with the crustose and gelatinous rock-lichens of Bermuda (see Bull. Torrey Bot. Club 43: 146–155. 1916). Such rock-lichens as occur on St. Thomas belong to widely distributed groups even where the actual species are more restricted in distribution. In fact the greater part of the lichen-flora is made up of species more or less common throughout the West Indies or even in the tropics of both hemispheres. It is probably safe to say that there are not more than half a dozen endemic species in St. Thomas. Of the three new species described in this paper, two occur elsewhere in the West Indies. The flora is comparatively rich in the variety of crustose bark-lichens, especially in the genera *Anthracothecium* with 5 species, *Arthonia* with 8 species, and *Opegrapha* with 5 species. It is rather surprising that only one *Graphis* and no *Trypethelium* should have been collected. On the whole the lichen-flora is rather commonplace. In the following list, stations outside of the Virgin Islands are noted for species, the range of which is limited or not well known.

### LICHENS OF ST. THOMAS

1. Dermatocarpon hepaticum (Ach.) Th. Fr. On soil, without definite locality, 151.

[16] Contributed by Lincoln W. Riddle, Wellesley College.

2. Leptoraphis epidermidis (Ach.) Th. Fr. On bark, Bordeaux, 1381.
3. Porina desquamescens Fée. Without data, 1288a.
4. Porina nucula Ach. On *Erythrina*, St. Peter, 1444b, 1445.
5. Pyrenula leucoplaca (Wallr.) Koerb. On bark, Smith's Bay, 1276a.
6. Anthracothecium Breutelii Muell. Arg. Flora **68**: 339. 1885. On bark, without definite locality, collected by Breutel. Endemic.
7. Anthracothecium canellae-albae (Fée) Muell. Arg. On *Cephalocereus*, Smith's Bay, 1274a; on twigs of *Guettarda*, Crown, 450 m. altit., 1357. South America.
8. Anthracothecium libricolum (Fée) Muell. Arg. On *Melicocca*, Tutu, 468a; on same, Smith's Bay, 1276, 1282; on *Erythrina*, St. Peter, 1444.
9. Anthracothecium ochraceoflavum (Nyl.) Muell. Arg. On bark of coconut palm, near Charlotte Amalia, 489; on *Trichilia*, Tutu, 467.
10. Anthracothecium pyrenuloides (Mont.) Muell. Arg. On bark, without definite locality, collected by Dr. Forel. Recorded by Nylander in Flora **63**: 127. 1880.
11. Melanotheca foveolata Muell. Arg. On bark, near Tutu, 1287. Cuba.
12. Parathelium indutum Nyl. On *Cephalocereus*, Smith's Bay, 1274; on bark, Bordeaux, 1382 in part. Porto Rico, Colombia.
13. Parmentaria astroidea Fée. On bark, Bordeaux, 1382 in part.
14. Arthonia anegadensis Riddle Mem. New York Bot. Gard. **6**: 579. 1916. On *Bontia*, Smith's Bay, 1286. Anegada.
15. Arthonia conferta (Fée) Nyl. On *Plumeria*, Tutu, 1484.
16. Arthonia gregaria (Weig.) Koerb. On bark, Bordeaux, 1380.
17. Arthonia ochraceella Nyl. On bark of old fallen branch, Crown, 450 m. altit., 1362. Cuba.
18. Arthonia rubella (Fée) Nyl. On *Melicocca*, Tutu, 468b.
19. Arthonia subrubella Nyl. Collected by Dr. Forel. Recorded by Nylander in Flora **63**: 127. 1880.
20. Arthonia.[17] On *Guilandina*, Smith's Bay, 1281 p.p.
21. Arthonia. On *Plumeria*, Tutu, 463.
22. Arthothelium macrothecum (Fée) Mass. On mango, St. Peter, 1247.
23. **Opegrapha acicularis** Riddle **sp. nov.**

Thallus epiphloeodes crustaceus effusus determinatus nigrolimitatus, albidus

[17] There are included in this paper three species of *Arthonia* the determination of which it has not been possible to complete in the time at my disposal. L. W. R.

vel albo-cinerascens, tenuis laevis subcontinuus. Apothecia sessilia nuda ad 0.8 mm. lata, primum orbicularia suburceolata, margine crenato, dein orbicularia oblonga vel subdifformia, disco late aperto plano rugoso atrofusco, margine laciniato partim stellato-radiato nitido nigro; epithecio fusco; hymenio incolore, 120–130 $\mu$ altit.; hypothecio incolore; amphithecio sub lamina deficiente, cetero crasso nigro. Paraphyses firmae crassae ramosae haud connexae. Asci cylindrices, 8-spori. Sporae incolores aciculares rectae vel subflexuosae vel rarius contortae, 20–24-loculares, cellulis cylindricis, 60–100 x 2–3 $\mu$.

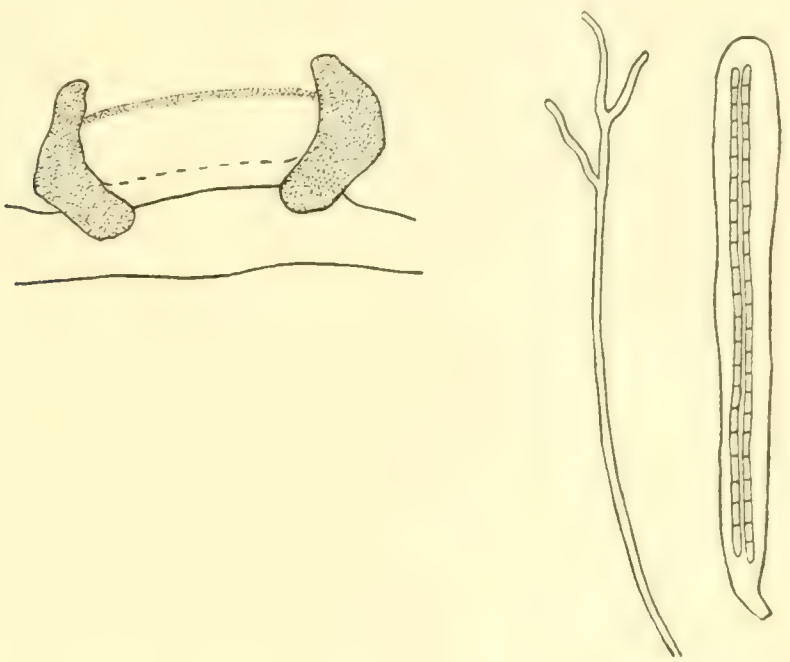


FIG. 1. *Opegrapha acicularis* Riddle. Vertical section of apothecium (stippling indicates dark coloration); paraphysis; ascus with two of the eight spores.

On bark of *Erythroxylon*, Punta Aguila, Porto Rico, collected by N. L. Britton, J. F. Cowell, and Stewardson Brown, Feb. 27, 1915, no. 4682 (**type**!). Also, on *Guilandina*, Smith's Bay, St. Thomas, 1276a, 1279; and on *Coccolobis*, Great Harbor Cay, Berry Islands, Bahamas, N. L. Britton and C. F. Millspaugh, no. 2545.

This is a striking and distinct species belonging to the section *Pleurothecium* of the genus *Opegrapha*. Externally it is easily recognizable by the marked tendency for the laciniate margin of the apothecia to spread out in a stellate manner. The spores resemble those of *Lecanactis myriadea* (Fée) Zahlbr. and of *Opegrapha pleistophragmoides* Nyl. But both of the species named have the black amphithecium complete at the base, and the spores are almost twice as thick.

24. OPEGRAPHA AGELAEA Fée. On *Crescentia*, Tutu, 462. Cuba, Colombia.

25. OPEGRAPHA ATRA Pers. On *Guilandina*, Smith's Bay, 1278a; on *Melicocca*, Smith's Bay, 1285.

26. Opegrapha Bonplandi Fée. On *Melicocca*, Magen's Bay, 1310; on bark, Mariendahl Road, 1476.
27. Opegrapha vulgata Ach. On *Melicocca*, Tutu, 468.
28. Graphis scripta (L.) Ach. On bark, Smith's Bay, 1277.
29. Phaeographis inusta (Ach.) Muell. Arg. On *Acacia*, near Charlotte Amalia, 486; on *Guilandina*, Smith's Bay, 1278; without locality, 464.
30. Chiodecton (Sect. Enterographa) sp. On *Erythrina*, St. Peter, 1445a.
31. Gyrostomum scyphuliferum (Ach.) Fr. On *Plumeria*, Tutu, 465; on *Acacia*, near Charlotte Amalia, 487, 494.
32. Bilimbia cuprea Massal. in Lotos (1856) 77.
    *Lecidea cupreorosella* Nyl. Mem. Soc. Sci. Nat. Cherb. 5: 122. 1857.
    *Biatora cupreorosella* Tuck. Syn. N. A. Lich. 2: 34. 1888.
    On old brick, St. Peter, 1442. Eastern United States, Europe.
33. Bacidia albescens (Arn.) Zwackn. On *Erythrina*, St. Peter, 1445b.
34. Cladonia pityrea f. squamulifera Wainio. On rocks, slope of Crown, 1440.
35. Leptogium chloromelum (Sw.) Nyl. On bark, Cowell Point, 103, 172; on *Pisonia* roots, Water Island, 153.
36. Leptogium tremelloides (L. f.) S. F. Gray. On tree-trunk, Crown, 1361.
37. Leptogium tremelloides var. caesium (Ach.) Hue. On rock near Bonne Resolution, 447.
38. Lecanora cinereocarnea (Eschw.) Wainio. Without data, 23a; on *Guilandina*, Smith's Bay, 1281.
39. Lecanora granifera Ach. On bark, Mariendahl Road, 1476a.
40. **Lecania euthallina** Riddle **sp. nov.**

Thallus crustaceus uniformis effusus crassus rimoso-areolatus, areolis 0.2–0.4 mm. latis leviter convexis contiguis, cinereus vel sat pallide fuscescens; hypothallo nullo. Gonidia cystococcoidea. Apothecia 0.6 mm. (0.4–1.0 mm.) lata, numerosa partim caespitosa superficialia sat elevata regularia, disco concavo castaneo vel fusco-nigricante nudo, margine proprio tenue disco concolore, margine thallino integro vel demum crenulato crasso prominente thallo concolore; epithecio fulvo; hymenio et hypothecio incolore. Asci 8-spori. Sporae incolores oblongae biloculares haud placodiomorphae, 10–12 x 4–5 μ.

On rock, Tutu, St. Thomas, collected by Dr. N. L. Britton, Mrs. E. G. Britton, and Miss Delia W. Marble, Feb. 8–9, 1913, no. 469 (**type**!).

*Lecania euthallina* differs from *L. erysibe* (Ach.) Th. Fr. in the much better developed thallus (whence the specific name), it being compact,

thicker, and more continuous. Furthermore, the apothecia are more concave, with the persistent thalline margin more conspicuous.

41. PARMELIA CETRATA f. SUBISIDIOSA Muell. Arg. On tree-trunk, Crown, 1441 in part. North Carolina, Florida, Cuba, Jamaica.
42. PARMELIA CONSPERSA (Ehrh.) Ach. On rocks, Crown, 450 m. altit., 1358.
43. PARMELIA LATISSIMA var. CRISTIFERA (Taylor) Hue. On tree-trunk, St. Peter, 1249; on twig, Crown, 1441 in part.
44. PARMELIA PERLATA (L.) Ach. On rocks, near Bonne Resolution, 446; on *Spondias*, Mandal, 1311.
45. RAMALINA COMPLANATA (Sw.) Ach. Without data, 1356a.
46. RAMALINA GRACILIS (Pers.) Nyl. On twigs of *Guettarda*, Crown, 450 m. altit., 1356.
47. **Blastenia nigrocincta** Riddle **sp. nov.**

Thallus crustaceus arcte adnatus sat crassus, ambitu subradiato-laciniatus effiguratusque, centro rimoso-areolatus, areolis 0.4–0.8 mm. latis leviter convexa primum contiguis demum hypothallo nigro dispersis, cinereo-albescens dein fumosus aut partim luridus. Apothecia 0.3–0.5 mm. lata, superficialia dispersa vel partim caespitosa nuda, disco plano vel leviter convexa ferrugineo-aurantiaco, margine proprio sat tenue persistente nigro nitido, margine thallino nullo; excipulo externe coeruleo-nigro interne incolore; epithecio ferrugineo; hymenio incolore; hypothecio pallide fuscescente. Asci 8-spori. Sporae incolores ellipsoideae biloculares placodiomorphae, loculis poro tenue confluentibus, 12–14 x 5–6 $\mu$.

On rock, Tutu, St. Thomas, collected by Mrs. E. G. Britton and Miss Delia W. Marble, Feb. 8–9, 1913, no. 469a (**type**!). Also, on limestone, Montalva, Porto Rico, N. L. Britton, J. F. Cowell, and Stewardson Brown, March 2–4, 1915, no. 4810.

This species is distinct in the contrasting coloration of the black margin and the orange disk of the apothecia, a character which will serve to distinguish it on the one hand from species with similar thalline characters, such as *Bl. Forstroemiana* (Fr.) Muell. Arg.; and on the other hand from *Bl. ferruginea* (Huds.) Koerb., where the disk and margin are concolorous, and from *Blastenia peragrata* (Fée) Muell. Arg., where the margin is black, but the disk is aeruginous-brown.

48. **Caloplaca diplacia** (Ach.) Riddle **comb. nov.**

*Lecanora* Ach. Synop. Lich. 154. 1814.

On rock, near Charlotte Amalia, 493, 495, 1485 in part. Also recorded by Nylander in Flora **63**: 127. 1880. Apparently confined to the West Indies.

49. CALOPLACA MURORUM (Hoffm.) Th. Fr. On rock, near Charlotte Amalia, 1485 in part.

50. **Caloplaca subsequestra** (Nyl.) Riddle **comb. nov.**
*Lecanora* Nyl. Flora **63**: 127. 1880.
On rocks, without definite locality, collected by Dr. Forel. Endemic.

51. Buellia discolor (Hepp) Koerb. On rock, Tutu, 469b; without definite locality, collected by Dr. Forel, according to Nylander (l. c.). Europe.

52. Buellia parasema var. aeruginescens (Nyl.) Muell. Arg. On coconut near Charlotte Amalia, 489a.

53. **Buellia prospersa** (Nyl.) Riddle **comb. nov.**
*Lecidia* Nyl. Flora **63**: 127. 1880.
On rocks, without definite locality, collected by Dr. Forel. Endemic.

54. Pyxine cocoes (Sw.) Nyl. On bark, near Bonne Resolution, 445; on *Melicocca*, Tutu, 466.

55. Pyxine cocoes var. endoxantha Muell. Arg. On *Guilandina*, Smith's Bay, 1280; on bark, Mariendahl Road, 1475.

56. Pyxine Meissneri Tuck. On coconut palm, without definite locality, collected by Dr. J. N. Rose, 3198.

57. Physcia alba (Fée) Muell. Arg. On *Erythrina*, St. Peter, 1443.

58. Physcia caesia (Hoffm.) Nyl. On rocks, without definite locality, collected by Dr. Forel. Recorded by Nyl. Flora **63**: 127. 1880.

59. Physcia crispa (Pers.) Nyl. On *Elaphrium*, near Charlotte Amalia, 491; on roots, same locality, 492, 496; on *Melicocca*, Tutu, 461.

60. Physcia erosula Nyl. Flora **63**: 127. 1880. Based on material growing on rocks, St. Thomas, without definite locality, collected by Dr. Forel. Doubtfully distinct from the widely distributed *Physcia tribacia* (Ach.) Tuck.

61. Physcia picta (Sw.) Nyl. On rock, St. Peter, 1260; on coconut palm, collected by Dr. J. N. Rose, 3197.

62. Physcia speciosa (Wulf.) Nyl. On rocks, near Charlotte Amalia, 405; on bark, St. Peter, 1248, 1250.

## LICHENS OF ST. JAN

1. Pyrenula mamillana (Ach.) Trev. On bark of *Icacorea*, Bordeaux, 597.

2. Melanotheca Achariana Fée. On *Inga*, Bordeaux, 598. Cuba, Venezuela.

3. Mycoporellum ellipticum Muell. Arg. Flora **72**: 508. 1889. On bark, without definite locality, collected by Levier, no. 113. Endemic.

4. Arthonia. On bark, Bordeaux, 577.
5. Arthothelium macrothecum (Fée) Mass. On *Icacorea*, Bordeaux, 540.
6. **Graphina nitidescens** (Nyl.) Riddle **comb. nov.**
   *Fissurina* Nyl. Lich. Japon. 108. 1890.
   On *Nectandra*, Bordeaux, 581. Florida, Cuba, Porto Rico.
7. Opegrapha vulgata Ach. On *Maytenus*, Little St. James Island, N. L. Britton & J. N. Rose, 1405.
8. **Leptogium marginellum** var. **isidiosellum** Riddle **var. nov.**
   Thallus isidiis tenuibus dense tectus; ceterus ut in forma typica apothecia nulla.
   On wet rock, road to Rosenberg, N. L. Britton & J. A. Shafer, Feb. 5–7, 1913, no. 276 (**type**!).
   The fringed apothecia being such a characteristic feature of *Leptogium marginellum*, it is only after some hesitation that this material has been placed here. The texture and the wrinkling of the thallus is in exact agreement, however, with typical specimens. And the relation of this variety to the species is strictly comparable with the conditions in *L. tremelloides*, abundantly fruiting in the tropics, and its variety *caesium*, with isidia but very rarely fruiting; and with *L. phyllocarpum* and its variety *isidiosellum*.
9. Parmelia tinctorum Despr. On tree-trunk, Bordeaux, 567.

The following lichens are recorded in "Le Végétation des Antilles Danoises" by F. Børgesen & Ove Paulsen in Revue Générale de Botanique **12**: 507, 508. 1900.

Sticta Weigelii (Ach.) Wainio. St. Croix; St. Thomas.
Graphis scripta (L.) Ach. St. Croix.
Lecidea buelliana Muell. Arg. St. Croix.
Pertusaria Wulfenii (DC.) Fr. St. Croix.
Parmelia perlata (L.) Ach. St. Thomas; St. Jan.
Parmelia tinctorum Despr. [*P. coralloides* Mey. et Flot.] St. Croix.
Physcia integrata Nyl. St. Jan.
Rinodina sp. St. Croix.
Verrucaria sp. St. Croix.
Arthonia radiata (Pers.) Ach. St. Croix.
Schizoxylon sp. St. Thomas.

## Fungi

During our exploration of St. Thomas and St. Jan in 1913, about 25 species of fungi were obtained, and Dr. Rose collected four others on St. Croix; manuscript record has been made of these.

Twenty species collected by Mr. Ricksecker on St. Croix are

listed by Dr. Millspaugh in his "Flora of the Island of St. Croix," as determined by J. B. Ellis and F. D. Kelsey.[18]

Thirty-one species brought by various collectors to Copenhagen, determined by E. Rostrop, are recorded by Børgesen and Paulsen in their "Végétation des Antilles Danoises."

Seven species, collected on St. Thomas during the voyage of the "Challenger," are listed by M. J. Berkeley in Journal of the Linnean Society 14: 352.

These records duplicate each other considerably, indicating a known fungus flora of somewhat over fifty species only. Inasmuch as there must be several hundred species on the islands, a list of fungi is deferred for further mycological field work.

## Algae[19]

"The Marine Algae of the Danish West Indies" is the title of a work, now appearing in parts, in which Dr. F. Børgesen, of Copenhagen, is carefully describing and adequately illustrating the seaweeds of these islands. His adoption of the English language in this work makes it immediately serviceable to American students. Volume 1, including the Chlorophyceae (Green Algae) and Phaeophyceae (Brown Algae), was published in 1913 and 1914, and, at the date of writing, the first 240 pages of Volume 2, dealing with the Rhodophyceae (Red Algae) have appeared. Other papers of importance, dealing with the algae of the Danish West Indies, are the following:

**Borgesen, F.** A Contribution to the Knowledge of the Marine Alga Vegetation on the Coasts of the Danish West Indian Islands. Bot. Tidssk. **23**: 49–57. Figs. 1–4. 1900.

—— Et Bidrag til Kundskaben om Algevegetationen ved Kysterne af Dansk Vestindien. Bot. Tidssk. **23**: 58–60. 1900. [An abstract, in Danish, of the foregoing article.]

—— Contributions à la connaissance du genre *Siphonocladus* Schmitz. Overs. K. Danske Vidensk. Selsk. Forh. **1905**: 259–291. Figs. 1–13. 1905.

—— An Ecological and Systematic Account of the Caulerpas of the Danish West Indies. K. Danske Vidensk. Selsk. Skr. VII. 4: 337–392. Figs. 1–31. 1907.

—— The Dasycladaceae of the Danish West Indies. Bot. Tidsskr. **28**: 271–283. Figs. 1–9. 22 My 1908.

—— The Species of *Avrainvillea* Hitherto Found on the Shores of the Danish West Indies. Vidensk. Medd. Naturh. Foren. København **1908**: 27–44. pl. 33. Je 1908.

—— Some New or Little-known West Indian Florideae. Bot. Tidssk. **30**: 1–19. pls. 1, 2, Figs. 1–11. 23 O 1909; II. Bot. Tidssk. **30**: 177–207. Figs. 1–20. 9 D 1910.

—— Some Chlorophyceae from the Danish West Indies. Bot. Tidssk. **31**: 127–152. Figs. 1–13. 1911; II. Bot. Tidssk. **32**: 241–273. Figs. 1–17. 1912.

[18] The new species were described in Bull. Torr. Club **24**: 207–209. 1897.

[19] Contributed by Dr. Marshall A. Howe.

—— The Algal Vegetation of the Lagoons in the Danish West Indies. Biol. Arbejd. tilegn. Eug. Warming. 41–45. Figs. 1–9. 1911.

—— Two Crustaceous Brown Algae from the Danish West Indies. Nuova Notarisia 23: 123–129. Figs. 1–3. 1912.

—— The Species of *Sargassum* Found along the Coasts of the Danish West Indies, with Remarks upon the Floating Forms of the Sargasso Sea. 1–20. Figs. 1–8. 1914. [No. 32 of a Mindeskrift for Japetus Steenstrup.]

**Cleve, Peter Theodor.** Diatoms from the West Indian Archipelago. [Virgin Islands and St. Bartholomew.] Bih. Svens. Vet. Akad. Handl. $5^8$: 1–22 pl. 1–5. 1878. Annot. list.

**Dickie, George.** Marine Algae Collected at St. Thomas during the Expedition of H. M. S. "Challenger." Jour. Linn. Soc. Bot. 14: 312–313. 17 O 1874. List.

**Millspaugh, C. F.** Flora of the Island of St. Croix. Field Col. Mus. Bot. 1: 441–546. 1902. On pp. 467, 468 is a list of 17 species of marine algae, determined by Professor W. G. Furlow.

**Vahl, M.** Endeel Kryptogamiske Planter fra St. Croix. Skrivt. Naturh. Selsk. $5^2$: 29–47. 1802.

## ENDEMIC SPECIES

The approximate number of species native to the islands as recorded, excluding fungi and algae, is 1,052, as follows:

| | |
|---|---|
| Spermatophyta | 890 |
| Pteridophyta | 41 |
| Bryophyta | 46 |
| Lichenes | 75 |
| | 1,052 |

The numbers of Spermatophyta and Pteridophyta are not likely to be increased by further exploration, but there are probably some more Bryophyta and many more lichens to be obtained. As we know the flora at the present time, the following 27 species are endemic, at least to the Virgin Island group as a whole.

*Valota Eggersii* (Hack.) Hitchc. & Chase
*Agave Eggersiana* Trelease
*Peperomia myrtifolia* (Vahl) A. Dietr.
*Pilea Richardi* Urban
*Coccolobis Klotzchiana* Meissn.
*Zanthoxylum thomasianum* Krug & Urban
*Galactia Eggersii* Urban
*Malpighia pallens* Small
*Malpighia infestissima* (Juss.) Rich.
*Maytenus cymosa* Krug & Urban
*Reynosia Guama* Urban
*Sida Eggersii* E. G. Baker
*Psidium amplexicaule* Pers.
*Calyptranthes thomasiana* Berg.

*Eugenia sessiliflora* Vahl
*Chrysophyllum Eggersii* Pierre
*Forestiera Eggersiana* Krug & Urban
*Salvia thomasiana* Urban
*Physalis Eggersii* O. E. Schulz
*Solanum conocarpum* L. C. Rich.
*Wedelia cruciana* L. C. Rich.
*Phascum sessile* E. G. Britton
*Anthracothecium Breutelii* Muell. Arg.
*Lecania euthallina* Riddle
*Caloplaca subsequestra* (Nyl.) Riddle
*Buellia prospersa* (Nyl.) Riddle
*Mycoporellum ellipticum* Muell. Arg.

The endemic elements are, then, only about 2.6 percent. of the native flora. A few other species are almost endemic, being otherwise known only on Porto Rico or on some other neighboring island. There are a few endemic species known on Tortola, and one on Anagada, but if the native species of these two islands, additional to those of St. Thomas, St. Jan and St. Croix, were taken into account, the percentage of endemism would not be increased.

Porto Rico, with a very much greater area and much higher mountains, has about 13 percent of its species of Spermatophyta and Pteridophyta endemic.

# WEATHER CONDITIONS AND PLANT DEVELOPMENT

GEORGE P. BURNS

*Vermont Agricultural Experiment Station*

The effect of weather conditions on plant development has been one of the chief problems studied during the past few years by the ecologist, the agriculturalist, the forester and in some cases by the plant physiologist. The weather, however, is a variable mixture composed chiefly of different amounts of light—direct, diffuse, white, yellow, red, etc., or darkness; moisture—precipitation, humidity, soil-moisture, etc.; heat, temperature of the air and soil; wind, etc. Each of these component parts varies within short intervals of time and each has its effect direct or indirect on the living plants. The problems of the effect of weather conditions, then, is largely a physiological problem and such problems should be attacked only by means of accurate experiments under controlled conditions.

The ecologists have been attempting to change from the old descriptive methods in which the results of a more or less accurate study of the vegetation of a given area were published. Sometimes this study was accompanied by a few tables of meteorological data gathered from a nearby U. S. Weather Bureau station. In only a few cases were attempts made to relate these data to the descriptive part of the study and one was often at a loss to know why they were included in the publication. This type of work has served a good purpose in a preliminary way but is now outgrown. More accurate methods have been introduced by advanced workers and ecologists have adopted the plan of gathering their own data with instruments placed in the field, the attempt being made to place them under the same weather conditions as those of the plants under consideration.

The largest amount of data has been collected on evaporation rates by workers with atmometers. This is probably due to the fact that these instruments are inexpensive as compared with the cost of the recording instruments necessary for collecting other data. But they lack standardization, many kinds, shapes and sizes being in use. Since no atmometer can be made to work exactly as a plant, ecologists should adopt arbitrarily one type in order that data wherever collected may be compared. Some ecologists have gone deeply into this phase of the work and are well equipped with field instruments record-

ing soil temperature, air temperature, humidity, number of hours of sunshine, wind velocity, precipitation, evaporation, etc.

The fundamental problem, however, presents itself after the analysis has been made of the elements which enter into the compound "weather." It is the experimental determination of the effect of those elements, singly and collectively, as measured by the data compiled, upon the physiological activities of the plant under consideration. This effect can only be measured by means of accurately conducted experiments in which very expensive apparatus is used. One of our problems is so to outline the work and to set forth its fundamental importance that those in authority will be moved to purchase the ecological equipment without which these agricultural and silvicultural problems cannot be studied.

In the attempt to solve the problem above outlined some workers have used a "plant instrument." A given kind of plant has been grown by the side of atmometers, etc., at stations established under different climatic conditions and an attempt has been made to interpret their effect as registered by the "plant instruments." As an illustration of the attempt to interpret meteorological data in terms of plant development let us take the work dealing with temperature. One method contemplates the subtraction of a constant from the temperatures recorded and considers that thermometric degrees in excess of this constant are available for purposes of plant development. A second method seeks to express growth-rate in terms of the velocities of chemical reactions. A third—the physiological method—attempts to take into account the optimum and maximum temperatures as related to plant growth, and the attempt has been made to develop one formula which will express the combined effect of rainfall, evaporation and temperature on plant growth. This represents but little more than an attempt to show what might be done if we had sufficient experimental data on the reaction of plants to the complex conditions known as the weather.

Much of this work has been based on averages—averages for a month, a year, or a number of years. We read that a large amount of data assists in "smoothing out the curve" or that the "spasmodically jerky graph may be smoothed." It is certainly true that in some cases the curve should not be smoothed out, because it is the spasmodic graph that shows sudden changes and the extremes. The burden of this paper is to show that, in some cases at least, averages for long periods are of little value as compared to the importance of the data obtained for certain critical periods in the conditions of the environment as shown by the "spasmodic graph." Data collected for a short period in the summer may be very important, but are by

no means as valuable as those gathered by recording instruments during long periods of time. These latter data are valuable, however, primarily because they cover critical periods during which the environmental conditions are most severe for plant development. The limiting factor is not the average for the long period, but the maximum or minimum for any factor or group of factors during certain critical short periods of the longer season under consideration. This may be made more clear by illustration. The effect of shade on the development of white pine seedlings was under study. Lath shades known as "full-shade" and "half-shade" were used. It was found that germination took place sooner and that larger numbers of seedlings were produced in the "no-shade" bed than in those partly or fully shaded. The temperature of the soil was the controlling factor. The average soil temperatures computed from readings recorded every two hours with a Friez machine for the 24 days during the germination period were "full-shade" 47° F., "half-shade" 46.8° F., "no-shade" 49° F. These differences are too slight to have been responsible for the observed differences in germination. If we look at averages only and shut our eyes to the daily fluctuations we would conclude that soil temperature was not the controlling factor. When, however, the records were examined for extremes it was found that on certain days temperature variations occurred of as much as 20° F. as between the soils of the different beds, the soil of the "no-shade" bed reaching 73° F. It is easy to believe that such differences may constitute a controlling factor, in view of the fact that Atterberg has shown that this temperature is about the optimum for germination of these seeds.

One evening the nursery foreman reported that every seedling in our nursery was dead. Examination showed that the white pine leaves which the day before had been a beautiful green were brown and apparently dead. A closer study showed that the ends of the leaves including about one third of the leaf were dead. However, very little of this leaf browning occurred in another nursery located near a river bank, protected from the prevailing wind and on a richer soil. In the upper nursery where the browning occurred we had a number of recording instruments but unfortunately none in the lower nursery. The records show: that three slight showers and one heavy rain (1.28 inches) had fallen just previous to the appearance of the trouble; that for five days the sun had shown from nine to twelve hours daily; that a very heavy wind blew for three days before, especially while the sun was shining; that the humidity dropped daily below 50 percent, one day reaching 35 percent; that the air temperature was usually below 75° F.; that slightly protected areas in the upper nursery showed less damage than did the rest of the nursery.

It is of course impossible with any degree of certainty to determine from these data why the trees in one nursery suffered severely, whereas those in the other nearby location were but slightly affected. However, if one were to hazard a guess he might say that it was due to excessive transpiration, the chief immediate factor being differences in wind velocity. A similar result has been obtained experimentally when trees which have been shaded were suddenly exposed to sun and wind. The next day they showed "tip-burn" of the pathologists, or a "physiological disease" whatever that may be. One fact is clear. The death of the leaves was not due to the average conditions prevailing during the summer.

During the winter months the average soil temperatures in the nursery for depths of three, six and twelve inches were 35.8° F., 37.9° F., and 38.5° F. Each figure is the average of 2,100 readings taken every two hours from the record made by a Friez machine. They show little differences in temperature at the various depths given. When, however, the record is examined for critical periods it is found that probably the most important season was that from March 28 to April 18. During this period of 21 days the soil three inches deep froze and thawed sixteen times, at six inches, nine times and at twelve inches four times. Similar data collected in the adjacent forest showed that the soil both at six and at twelve inches thawed only once. We have no experimental data which determine the physiological meaning of these facts, but it is easy to surmise that in studying the effect of soil temperatures on plants we will not go far afield if we study carefully conditions obtaining during these critical periods as well as indeed full more than the general averages for the entire winter.

Numerous examples could be given to show that averages extending over long periods for humidity, sunshine, wind, air temperature, etc., not only explain little but, on the other hand, conceal the essential facts. In all study of the relation of weather conditions to the development of plants the importance of critical periods in the environment must be taken into consideration.

# MODERN APPLICATIONS OF BOTANY

MEL T. COOK

*New Jersey Agricultural Experiment Station*

It is very doubtful if any science is so thoroughly misunderstood by the public as the science of botany. To the average layman it is usually a study of flowers which usually involves harmless collections, classifications and mysterious Latin names; a study for the faddist; a study without applications of any value whatever. It is strange that a subject dealing with organisms upon which we are dependent for practically all of our food, clothing and fuel, a large part of the material for building and the manufacture of useful implements of various kinds, and most of our drug products should be so misunderstood. Yet, even the educated layman knows more about the Panama canal than he does about wheat, more about flying machines than he does about potatoes, and more about the Woolworth building than he does about cabbage. The names of great and near great military leaders, statesmen, ministers, physicians, architects, theatrical stars, ball players and pugilists are familiar to those millions, while very few can name a single person who has contributed to the feeding and clothing of mankind. In fact, few people, even among the educated classes, realize that agriculture, horticulture and forestry are in reality specialized branches of botany.

A brief statement of the early history of the subject may offer an explanation of this anomalous position of our science. Botany had its rise in the development of the medical professions, in the efforts of the practitioner to determine the uses of plants in the art of healing. This resulted in the study of local flora of a number of the most advanced countries and also the search for plants in foreign countries. Very naturally, the great number of species of plants forced these early students to formulate some system of classification whereby their materials might be catalogued. With their increasing knowledge of these species, it became necessary to devise new systems until finally this phase of the subject became all important. In the meantime, the medical profession gradually discontinued the use of the less important of the medicinal plants for those that were most easily obtained, most economical in preparation and most efficacious in use. A little later, we find the physician studying the crude drug and

a little later the prepared drug and paying little or no attention to its origin. Thus the two professions developed along diverging lines.

In the meantime, the invention and development of the microscope opened new and interesting fields to the botanists as well as to other scientists and also resulted in the rise of bacteriology, which has had such a marked influence on many lines of work, especially medicine.

At the same time the scientific study of agriculture was beginning to attract attention but, unfortunately, it is not an outgrowth of botany. Chemistry became the first sponsor for this new field of research and the first directors of many of our American agricultural experiment stations were chemists; they studied the soils and developed formulas for fertilizers—for what? To make plants grow, to increase plant production, and thus the problem of plant growth was taken by the chemists instead of the botanists.

Horticulture was very closely associated with botany and the developments of horticulture and botany were combined in many of our agricultural colleges. In many cases these soon came to be known as departments of horticulture, the botany becoming a vanishing factor; but in later years botany has re-entered these colleges as an independent, but in many cases a secondary subject. In those agricultural colleges in which botany has had a continuous existence, the lines of research were by no means the same. In some cases, they studied weeds and devised methods for their control; in others, they co-operated with the horticulturists in the study, introduction and improvement of valuable food and fiber plants; in others they studied the causes and methods of controlling plant diseases, but in many cases the second phase of the subject was quickly taken over by the now independent departments of horticulture.

It is impossible to tell just what the result would have been if our botanists of a quarter of a century ago had been as energetic in the development of the applied side of botany as the chemists were in the development of the applied side of chemistry. But it is reasonable to suppose that the results would have been similar, and that we would have today, not only the applied phases of botany, but we would also have far more workers on technical problems.

The future of botany in America is brighter that at any time in its history. It is a recognized subject in our universities, in arts and in agricultural colleges. It is recognized, both as a cultural subject of great value and interest and as a science with a direct bearing on the affairs of mankind. The botany of today means not only taxonomy, morphology, cytology and physiology as purely scholastic subjects but all in their relation to applied plant physiology, plant breeding and plant pathology with a direct bearing on horticulture, agronomy and forestry.

Plant growth is no longer a problem for chemists but for the plant physiologist, who is trained not only in botany, but in chemistry, physics and geology. Plant physiology has outgrown the expectations of its most enthusiastic devotees of a decade ago, and no one can foretell its future. It will doubtless result in important changes in agricultural methods.

Plant breeding, along the lines of artificial selection, is very old; in fact, it must have originated with the first steps in civilization. Many of our valuable economic plants were selected, grown and used by man before the beginning of written history and many improved varieties have been developed by self-taught, practical workers, men of great natural endowments and keen powers of observation. However it is none the less true that they are the products of the workings of natural laws and that a knowledge of these laws enables the present generations to work more rapidly than their ancestors. Many of our modern plant breeders are very properly more interested in researches leading to a knowledge of these laws than in their application. A law fully established and well understood will very soon be utilized by those interested in increased production. But the breeder should not loose sight of the very great value of plant breeding to agriculture. The final and true standard of measure of the value of any science must be in terms of its contributions to the welfare of mankind.

Plant pathology is one of the last of these branches of applied botany to be considered. It had its rise in the taxonomic study of fungi, many of which were recognized as the causes of plant diseases. Therefore, this study very naturally led to the study of methods of control. Indefinite and uncertain methods for the control of plant diseases have been used from time to time for more than a century. But a lack of definite knowledge of the causes and the physiology of these diseases and the actions of the remedies made the results very uncertain and very soon led to their disuse.

Modern plant pathology had its beginning in the works of de Bary and Berkeley, but did not make much progress until the latter part of the last century. The progress during the last decade has been rapid and has emphasized the necessity of many lines of study, such as a more thorough knowledge of the life history and taxonomy of the parasites, a knowledge of the physiological factors influencing both host and parasite and a knowledge of the physiological effects of the fungicides. It is also extremely important that we make extensive investigations on that ever increasing number of diseases which cannot at this time be attributed to any definite organism.

The prosecution of these lines of investigations means more in-

tensive researches in the taxonomy, morphology and physiology of the fungi and other organisms that cause diseases; in the morphology and physiology of the flowering plants; and plant breeding. The directing ideal in physiology and plant breeding must be the improvement of the plant for economic purposes, the development of resistance to disease and the increase in plant production.

Many phases of plant pathology are practically untouched. The greatest advancement has been made in the study of the diseases of orchard fruits, much has been done in the study of cereals, shade and forest trees, and certain truck crops, such as potatoes. While much work still remains to be done on the diseases of these crops, much more is necessary on miscellaneous truck crops and on ornamentals. The fact that truck and ornamental crops are grown under glass presents new and complicated problems of the greatest economic importance.

Many people, even botanists, have the idea that all phases of applied botany must be restricted to agricultural colleges. This is an unfortunate error which tends to broaden the gap between the botany on one side and horticulture, agronomy, forestry, etc., on the other. Only recently, a well-known government plant pathologist told the speaker that he had no great difficulty in securing young men trained in plant pathology but that, unfortunately, many of them were not trained in botany. Applied botany is in very great need of workers who have a thorough fundamental training in botany plus a specialized training in applied botany. Much of this work can be done to an advantage in our universities provided the proper viewpoint can be obtained. I use the term "viewpoint" guardedly, for while it is true that many of our workers in applied botany are poorly trained in fundamental botany, it is also true that many of our university men are about as well fitted for applied botany as the students of Hebrew. It has been said that no one can apply a science unless he has learned the science, but it is equally true that some learn a science that cannot be applied. The suggested applications in some technical papers compare very favorably with the comic sheet in the Sunday papers.

But the few lines of work indicated in this paper do not include all that are open to the botanists. Many of the manufacturing industries are needing, and will need for years to come, many men trained in botany and biochemistry. Some time ago the writer was asked to recommend such a man to make investigations on cellulose. Failing to find such a man, the company employed a chemist. The manufacture of rubber is another industry in which the services of a properly trained botanist can be very useful. And there are many

other lines of work too numerous to mention in the short time available for this paper. Furthermore, in the very near future, America may be called upon to furnish botanical workers for the world. A prominent London journal has already called attention to the necessity for the development of the agricultural resources of Great Britain's colonies, and admitted that the workers must come from America. The great resources of South America are practically undeveloped. Thus far, those countries have called on European countries for most of their workers, but in the near future they will probably turn to this country. With the close of the great international war, now in progress, the United States will probably become the great education center of the world, but we must give educational work largely along industrial lines. Are the American botanists prepared to meet the new demands?

# STUDIES IN THE GENUS GYMNOSPORANGIUM—I. NOTES ON THE DISTRIBUTION OF THE MYCELIUM, BUFFER CELLS, AND THE GERMINATION OF THE AECIDIOSPORE

B. O. DODGE

*Columbia University*

The sporophytic mycelium of different species of *Gymnosporangium* exerts an influence in connection with the growth of the tissues of the cedar hosts which is manifested in a variety of ways. It is not clear just why one species will cause the formation of a rather fleshy gall, while another species will lead to the development of a witch's-broom or a hard, woody burl. A study of the interrelationships of host and parasite, especially the more intimate association of the hyphae and the host cells may help to solve some of these interesting questions.

I wish to report briefly at this time the results of some studies made to determine: (1) the distribution of the mycelium in an infected leaf; (2) the possibility of its spread from leaf to stem; (3) the degree to which it spreads up and down; (4) its distribution in wood, phloem and cortex; (5) the distribution of haustoria. Four-nucleated aecidiospore germ-tubes of *Gymnosporangium transformans*, and the formation of buffer cells in the teleutospore sori of *G. fraternum* and *G. transformans* will be noted.

Farlow[1] determined the general distribution of the mycelium in the host for a number of American *Gymnosporangia* and described with considerable clearness the primary effects of the parasites on the tissues of the host plants. He found that the burls on *Chamaecyparis* infected by *G. biseptatum* are probably the result of a stimulation of the cambium by the hyphae mainly distributed in the cambium region. There appeared to be very little in the nature of a deleterious effect of the parasite on this host. It was evident to him, however, that the actual presence of mycelium in a given tissue is not necessary to account for distortions or abnormalities. In *G. Ellisii* the fungus interferes with the normal growth of the host, producing proliferations and swellings of the stems and branches. This may be due to a disturbance in the nutritive processes, the primary cause of which may

[1] Farlow, W. G. The *Gymnosporangia* or Cedar Apples of the United States. Am. Mem. Boston Soc. Nat. Hist. 1–38. *pl. 1, 2.* 1880.

lie at some distance. Farlow noted that the hyphae of this species are exceptionally large and that the brown mycelium runs down into the wood and along the medullary rays and also makes other brown patches extending some distance in circular areas between the annual rings. The greater part of the mycelium is found near the cambium and large masses of it are collected at points in the bark in preparation for the formation of sori.

Wörnle[2] made an extensive study of the relationships of host and parasite in nine species, and his report published in a forestry journal furnishes a valuable contribution on the subject. He endeavored to determine the particular tissues with which the mycelia are associated and stated his conclusions with considerable positiveness. *G. Juniperinum* was of special interest to him inasmuch as he supposed that the sori found on leaves as well as those on small twigs belong to the species that produces larger sori on the main stems. He could see that the mycelium in an infected leaf was connected with that from a small twig. He also learned that the leaf form is perennial. Four successive cork callus formations were found in one case, showing that for four years a sorus had been developed at the same point on the leaf. In the stem-inhabiting type he found that the mycelium is present in the wood as well as in the bast and cortex. Radially placed strands of parenchyma accompanied by mycelium are common in the wood; "Schlafende Augen" he calls them. Hyphae are intercellular, and he noted in some cases the presence of haustoria. Although Wörnle was not himself clear regarding the relationship of the three forms of the rust which he called *G. Juniperinum*, he was inclined to believe that the fungus gains entrance through the leaves, the mycelium later running down the twigs and into the main stem, where it becomes firmly established. Fischer[3] has shown that this was a false assumption since Wörnle was dealing with at least two species, but the accuracy of Wörnle's observations is not questioned.

The mycelium of *G. clavariaeforme*, according to Wörnle, is not present in the wood, although considerable transformation of tracheid tissue is to be seen in infected stems; arcs and sectors of this tissue are replaced by parenchymatous cells. He found, however, no mycelium in such areas. As the mycelium is generally distributed in the cortex and bast, he assumes that the cambium is in some way stimulated to develop more than a normal amount of wood cells, some

[2] Wörnle, P. Anatomische Untersuchung der durch Gymnosporangium-Arten hervorgerufenen Missbildungen. Forst. Nat. Zeits. 3: 68–84, 129–172. 1894.

[3] Fischer, E. Studien zur Biologie von Gymnosporangium juniperinum. Zeits. Bot. 1: 683–714. *f. 1–8.* 1909; 2: 753–764. 1910.

of which are inhibited in their growth, lacking bordered pits and having thin walls, that is, are more in the nature of parenchyma. Wörnle was especially fortunate in having the opportunity for consultation with Hartig and Tubeuf in his work, but he was handicapped in studying American species by being restricted to a limited number of dried specimens. He agrees in the main with Farlow's account of the location of the mycelium in *G. biseptatum* and *G. Ellisii*, although he makes no mention of Farlow's work. He concludes further that the mycelium of *G. biseptatum* is intercellular and is entirely absent in the wood. The tracheids are somewhat irregular and have thinner walls than ordinarily. He found that the hyphae of *G. Ellisii* are about 8 $\mu$ in diameter and are present in the wood, bast and cortex. The brown hyphae are associated with brownish cells which together make easily recognizable patches. The mycelium here also is strictly intercellular. His study of a three year old stem of red cedar infected with *G. clavipes* disclosed the fact that the tissues of the host are only slightly affected. The mycelium is distributed not only beneath the sorus but in the whole periphery of the twig, especially in the bast region. The wood is entirely free from the fungus. Wörnle predicted that this rust must develop sori one year after inoculation because in this three-year-old stem he found traces of two former sori, one above the other.

Harshberger's account[4] of the relationships of hyphae and host cells deserves special consideration, inasmuch as it does not agree in certain important particulars with the statements made by Farlow and Wörnle. He finds that in *G. biseptatum* the mycelium is quite generally present in the wood region where he states the hyphae are for the most part strictly intracellular. They run down through the lumen of a tracheid, pass out through bordered pits, enter an adjacent tracheid, or move over to medullary ray cells which they penetrate and thus become established where they receive nourishment sufficient to maintain their perennial growth as the wood of the burl increases in diameter. He believes that the hypha actually in the lumen of the cambium cell is responsible for the stimulation of this cell to produce abnormal amounts of wood! He describes and figures these intracellular hyphae in much detail, especially the hyphae in longitudinal sections of wood. The explanations accompanying his figures leave no doubt of Harshberger's opinion regarding the identification and location of intracellular hyphae. He lays much stress on the presence of "plugged" tracheids. He believes that they are caused by the mycelium with which they are generally asso-

[4] Harshberger, J. W. Two Fungous Diseases of the White Cedar. Proc. Acad. Nat. Sci. Philadelphia **1902**: 461–504. *pl. 22, 23.*

ciated. Hyphae may sometimes be intercellular. Swollen and nodular hyphae are not infrequent. Harshberger questions whether haustoria are ever present. It is well known from the work of Hartig and others that hyphae of wood-destroying fungi are capable of boring through lignified cell walls. Such fungi obtain their nourishment by activities leading to the disorganization of wood cells. The rusts are highly parasitic and haustoria play an important part in their nutrition. It would be interesting to find that such trunk parasites as *G. biseptatum* and *G. Ellisii* are more like the common heart rot fungi than they are like other rusts where the hyphae crowd in between the cells or mass in the intercellular spaces. My own observations do not support several statements made by Harshberger.

### Gymnosporangium Ellisii

I have succeeded in infecting *Chamaecyparis* by spraying potted cedars with aecidiospores of *G. Ellisii* (*G. myricatum*). Several cedars naturally infected and bearing brooms of different ages have also been grown in pots, so that I have had an abundance of material in all stages of growth for study.

The sorus usually matures about twenty-one months after inoculation. Where young leafy branches have been infected we find that the sorus may break out either in the leaf axil or through the leaf itself. At this time there is very little distortion of the twig. The primordium of the axial sorus is partly in the tissue at the base of the leaf and partly in the stem cortex beneath. Where the sorus emerges through the leaf we find that there is an increase in the number of mesophyll cells and the sorus primordium is not far below the epidermis. Strands of hyphae can be traced down to the short vein and into the woody portion of the stem. Serial sections show that the mycelium does not travel up and down the stem very rapidly; in some cases only one or two cm. in the first two years. Where a rapidly growing main stem is infected the hyphae run as much as five cm. in the same time. Trunks thirty years old have been cut and one such shows traces of mycelium for a vertical distance of only about ten cm., although the fungus had been active during the life of the tree, thirty years. Sections taken from various parts of a small artificially infected plant bearing a dozen potential witches' brooms show that each broom will be the result of a separate infection. The mycelium does not enter at one point and spread through the entire plant. However, if the original infection should be at the growing point of the main stem a broom is formed that permanently dwarfs the plant. The mycelium invades every tissue except the cork. It is found in patches in all of the annual rings, and is espe-

cially abundant along some of the medullary rays. It is not evenly distributed. The hyphae seem to travel in fascicles and they are everywhere intercellular. Sections of the wood show that there are strands of parenchyma that, from appearances, would seem to be burrowing through the wood, thrusting the tracheids aside as though endowed with great power. These same parenchyma strands are also found in the cortex. They run in almost every direction. Hyphae are always associated with them. Tracheids in infected areas of the wood are considerably modified. The walls are thinner, the cells are prismatic and in many cases have failed to develop bordered pits. The walls of such cells frequently appear to be broken down or crushed in and partially disorganized. It may very well be that the fungus has some power to disorganize lignified cell walls. Wherever hyphae occupy the lumen of a cell it is likely to have been the result of such mass action. There is no boring through the walls nor entering tracheids through bordered pits. The "Schlafende Augen," or parenchyma strands, in the cortex and along the line of medullary rays in the wood as well as the patches of abnormal or partially developed tracheid tissue are the result of the stimuli proceeding from hyphae that were nearby at the time this tissue was being developed. It is difficult to understand how a cambium cell harboring a hypha could divide at all, or how a tracheid could change its form once it has become lignified.

The cambium reacts in such a way as to cut off by the excessive development of tracheids certain fascicles of hyphae and thus check the radial and longitudinal advances of the fungus. The apparently isolated patches of mycelium found in the heart wood are nevertheless quite generally connected above or below with some radially placed strand that ultimately reaches the cortex. This may be the main reason why one finds living hyphae deeply imbedded beneath several rings of wood.

Haustoria may occasionally be found in cells of the cortex medullary rays, but they are not abundant. Some of these haustoria are binucleated.

There seems to be no question that Wörnle was right in stating that the hyphae of *G. Ellisii* are intercellular.

### Gymnosporangium biseptatum

Harshberger and Wörnle disagree on a second important point in their studies of *G. biseptatum*. This relates to the presence or absence of mycelium in the wood cylinder of the cedar.

I have as yet been unable to infect the cedar with this species. I have studied specimens naturally infected and especially one from a

small plant which I was able to transplant and grow in the greenhouse. In 1915 this small burl bore two sori. The same burl bore six sori in 1916. The branch was six years old when cut. The mycelium spreads quite evenly through the cortex and is especially abundant beneath a sorus where we find one or two large haustoria in nearly every cortex cell. The medullary ray cells of the cortex are likewise attacked and the mycelium penetrates down to the cambium. The walls of the tracheids are somewhat thicker than usual, in this respect differing from the specimens examined by Wörnle.

I have been unable to find any intracellular hyphae, and in this six-year-old branch there are certainly no hyphae inside of the cambium ring, that is, in the wood cylinder, such as Harshberger describes. The most striking feature about this fungus is the great abundance of large haustoria found in nearly every cell of the cortex in the vicinity of a sorus.

### Gymnosporangium clavipes

The red cedar may be infected with *G. clavipes* without difficulty by spraying with aecidiospores. Plowright[5] states that it takes two years for *G. clavariaeforme* to mature sori, but Tubeuf[6] found that sori developed one year after inoculation of the juniper. My experience with *G. clavipes* may serve to explain this discrepancy.

On August 1, 1915, a small cedar was inoculated with *Gymnosporangium clavipes*. A few sori appeared in 1916 on what was, in 1915, the growing region of the main stem. In 1917 sori burst out quite generally over the plant. The question has arisen: Is it possible that from the original point of infection of 1915 the mycelium ran down the main stem out into the branches where further sori formed in 1917? Inspection showed that the sori were not evenly scattered along the branches, but appeared in groups with intervening spaces of some length between, varying from one to several cm. Serial sections of some of the smaller branches made at points between groups of sori do not show the presence of mycelium. For several inches near the top of the main stem the sori are so close together that mycelium appears to be continuous. It is noteworthy, however, that there are no sori on those parts of the plant that have grown since the plant was inoculated in August, 1915. The mycelium is intercellular and lies for the most part well out in the cortex just beneath the cork, some hyphal ends even pushing in between the inner cork cells. It may require only one year for full development at the

[5] Plowright, C. B. British Uredineae and Ustilagineae. 1893.

[6] Tubeuf, C. Mitteilungen über einige Pflanzenkrankheiten. Zeitschr. Pflanzenkr. 3: 201–205. 1893.

growing point where abundant food is available, or even take two years in regions less favorably located. The characteristically binucleated haustoria are of large size and are easily demonstrated.

I have examined several stems three years old but do not find that the mycelium spreads out through the entire cortex and into the bast as described by Wörnle. *G. clavipes* brings about less increase in development of wood tissue than *G. biseptatum*, but this may be due to the fact that the mycelium does not approach the cambium as closely. This species may develop strictly foliicolous sori in which case the mycelium is very limited in extent. The sorus is then not deep seated. Haustoria can be found in epidermal cells.

### Gymnosporangium transformans

I have previously reported[7] that two leaf-inhabiting species of *Gymnosporangium* can be distinguished on *Chamaecyparis*. The account of the cultures in support of this statement is being published in another paper. For convenience I shall call one form *G. transformans*. Its aecidial form is *Roestelia transformans* on *Aronia*. *Gymnosporangium fraternum* is an appropriate name for the second leaf form which infects *Amelanchier*. The aecidium is very similar to that of *Roestelia Botryapites;* I am not prepared to prove that it is *R. Botryapites*. A cytological examination of cedar leaves infected with *G. transformans* and *G. fraternum* reveals further characteristics by which they may be distinguished.

If we section a leaf of *Chamaecyparis* infected with *G. transformans*, we find that the mycelium is especially abundant in the large intercellular spaces of the spongy mesophyll and the hyphae push in between the cells of the palisade on all sides. No hyphae are to be found in the epidermis. If the section includes the short vein of the leaf we see that hyphae are prevented in some way from entering the vascular tissue. There is an irregular row of large cells surrounding the vein of the leaf. These pericycle(?) cells do not normally form a perfectly closed ring; it is occasionally broken by smaller supporting cells. In regions where the hyphae reach the large cells one can find, here and there, that they have been penetrated by one or two haustoria. Such infected cells are about one third larger than usual. The cytoplasm is rather dense, including considerable stored food and takes the gentian violet stain somewhat deeply. The nuclei appear to be quite normal. Haustoria are also occasionally found in mesophyll and palisade cells. The cells of the mycelium are binucleated and the nuclei stand out very clearly, especially where

[7] Dodge, B. O. Report on further cultures of Gymnosporangia. Paper read at the December meeting of the Botanical Society of America, New York, 1916.

leaves have been fixed at a time when the sorus is fully matured. The mycelium is confined to the leaf bearing the sorus and does not ordinarily invade the stem at any point along the line of attachment. The large cells surrounding the leaf vein appear to prevent the mycelium from entering the phloem of the stem.

At the point where the sorus is to be developed, we find a well-defined pseudo-parenchyma, the cell walls taking the orange stain. The upper cells of this pseudo-parenchyma are somewhat enlarged and elongated. These are likewise binucleated. They soon begin to swell, lose their cytoplasm, and the nuclei degenerate. In order to show these upper cells in this condition the material must be fixed at the earliest possible time that an infected leaf can be distinguished,

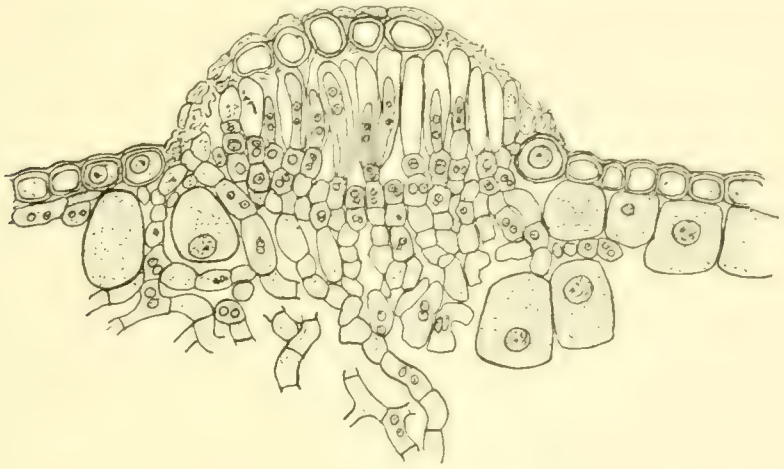
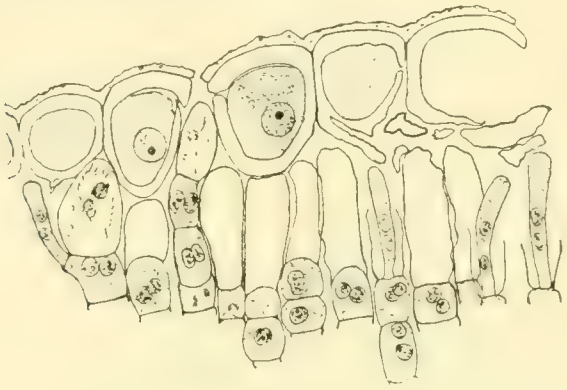


FIG. 1. Section of a sorus of *G. transformans* on a leaf of the southern white cedar at the narrowest portion of the young sorus. The epidermis is broken up on either side, only traces of the cuticle and fragments of the cell walls being visible. At the center epidermal cells are still visible. A number of buffer cells in various stages of degeneration can be seen, and binucleated teleutospore buds growing through the buffer cells are common.

that is, when a spot appears as a slight, waxy, translucent, light orange blister. In such cases the epidermis may not have been ruptured and fixation of the mycelium is not apt to be of the best, unless the leaf is cut through. The upper cells mentioned become mere bladdery sacs and during this process of swelling the inner walls of the epidermal cells, and hypodermal cells when present, are broken down either by enzyme action or by actual pressure, and the heavily cutinized epidermis is lifted up and split open (Text-fig. 1). The splitting usually occurs in a line along one side of the leaf, but very often the split runs longitudinally down through the middle. Sometimes two sori develop side by side on the same leaf. The bladdery cells evidently function as buffer cells to disrupt the epidermis. These buffer cells perhaps represent simply the first series of teleutospore mother cells

that are sacrificed in order that the epidermis may be broken open (Text-fig. 2). The true basal cells now grow out through the buffer cells, forming a club-shaped bud which soon becomes binucleated. These nuclei divide and the stalk is cut off; later three pairs of nuclei can be seen and the wall is formed between the two cells of the teleutospore (Text-fig. 3). Quite mature spores can be found along the line where the epidermis first ruptures and all stages in their development can be seen further back.



2

3

FIG. 2. A portion of a sorus of *G. transformans* showing two rather pointed buffer cells forcing epidermal cells aside, fragments of the walls of the epidermal cells lie just above the buffer cells at the right. Four young teleutospore buds are visible.

FIG. 3. Teleutospore of *G. transformans.*

The gametophytic stage on *Aronia* may sometimes attack the young stem, giving rise to an irregular herbaceous gall, which becomes covered with horn-like projections from which the aecidia arise. If such a plant is kept in the greenhouse all winter, aecidiospores will continue to be formed in some cases for several months after the leaves have fallen from the plant. These spores are regularly binucleated and possess 7 or 8 germ pores irregularly distributed (Pl. I, Fig. 1). The spores germinated on agar or water frequently form a swollen pouch near the tip of the germ tube. The nuclei of the spore push through the germ pore, apparently one closely following the other (Pl. I, Fig. 3). At the next stage we find two nuclei lying in the germ tube just outside of the pore (Pl. I, Fig. 4). These nuclei then migrate further out into the tube and come to lie in the swollen pouch (Pl. I, Fig. 5) where they presumably divide conjugately, since many cases have been observed where there were four nuclei, in pairs, lodged in this portion of the tube (Fig. 6). The germ tube now elongates rapidly and branches freely at the tip (Fig. 8). The four nuclei move forward and may lie along the tube in a row in the wider portion at the end or they may be distributed, one nucleus in each branch, or

two lying further back, the other two occupying separate branches. A cell wall is finally laid down, cutting off the outer portion of the germ tube containing the nuclei and most of the cytoplasm (Figs. 8–10). This curious method of germination is in no sense similar to the development of a promycelium, though four nuclei are produced in each case. It may be that it is fairly common among the rusts as Sappin-Trouffy has pointed out.[8] Whether or not it is possible to find an appropriate artificial medium for the development of the mycelium of a rust in artificial cultures, it would seem that such cases as these afford at least a starting point. Four-nucleated germ tubes are the rule in these cultures, but fully developed tubes with only two nuclei are not difficult to find (Fig. 11).

In some of my cultures in which the petiole of a leaf had been infected at the junction with the blade, it was found that the winter bud was larger than usual. The mycelium must have run down the petiole and become established in the bud. When such plants were put in the cold frame over winter and taken out in the spring, these buds developed small leaves which at once became evenly covered with spermogonia and later were transformed into large galls from which aecidia developed quite normally.

In some cases the mycelium seems to penetrate into the tissues of the stem where a spindle-shaped swelling or burl is formed. In the following spring a green gall bursts out through the cork, forming a nodular swelling outside and from this spermogonia and aecidia are produced. I have had several cases in which *Roestelia transformans* has survived the winter and developed aecidia the following spring The same is true in my cultures of *R. Botryapites*. In October, 1915, winter buds of six Amelanchiers showed signs of being infected. All of these survived the winter and developed spermogonia and ripened aecidiospores in the month of June, which is several months earlier than they can be found in nature. These are not cases where the formation of an aecidium has simply been delayed. On the contrary, an entirely new crop of spermogonia arises from newly formed tissue, new gall growth, and we find the aecidia developing as in normal cases of infection with sporidia.

### Gymnosporangium fraternum

The buffer cells in the teleutospore sori of *G. fraternum* are much more striking in appearance, forming as they do a perfectly even palisade layer that frequently extends entirely across the sorus without interruption (Text-fig. 4). This is a very characteristic feature of

[8] Sappin-Trouffy, P. Recherches histologiques sur la famille les Urédinées. Le Botaniste **5**: 59–244. *f. 1–69.* 1 D 1896.

the rust. The difference in the shape of the buffer cells of *G. transformans* and *G. fraternum* corresponds roughly with that between the teleutospores; they are comparatively long in the latter species.

On January 30, 1917 a potted plant naturally infected with *G. fraternum* was taken from the cold frame and examined. Several leaves showed by the presence of slight yellowish spots that they would develop sori. Sections of one leaf cut on this date showed

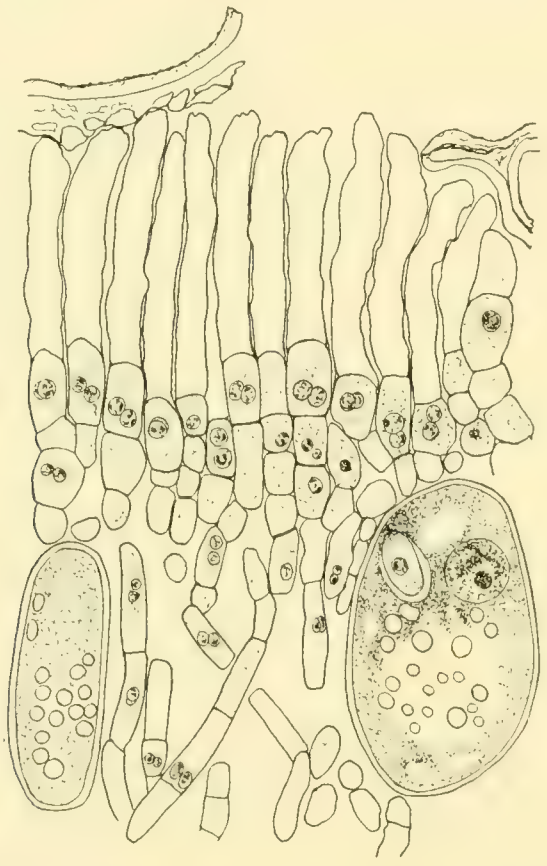


FIG. 4. Section of a leaf of the white cedar infected with *G. fraternum* showing the layer of buffer cells at the time when the epidermis has been quite completely disorganized. At the right a large palisade cell in the process of disorganization, but the nucleus is still visible and a haustorium is present.

that the pseudo-parenchyma or teleutospore primordium was well marked. The buffer cells were mostly without granular contents and nuclei (Text-fig. 5, *A*). In a few cases fragments of the degenerated nuclei could be seen. By February 2, a sorus taken from the leaf of the same plant showed great numbers of teleutospore buds in the 2- and 4-nucleated stages (Text-fig. 5, *C*). A few buds had 6 nuclei, and the stalk cells of these had been cut off. Buffer-cell walls were just visible as narrow irregular lines showing most distinctly at the base of the young teleutospore. Two days later, February 4, cross-walls had been formed in many spores but nuclear fusion had

not occurred (Text-fig. 5, *D*). Remnants of buffer-cell walls were now difficult to find. A mature spore is shown in Text-figure 5, *E*.

The mycelium of *G. fraternum* penetrates through the leaf in every direction. The mesophyll cells are usually somewhat enlarged and are packed rather closely together with small intercellular spaces. Haustoria are quite abundant in such cells. The cells surrounding the vein are especially affected. They appear to be filled with minute granules and as many as eight or ten haustoria can be found in a single cell, the more common number being two to four. A complete ring of these large cells is formed. This is due to an increase in number as well as their larger size. This, taken in connection with the increase in the mesophyll tissue, gives the leaf a slightly thicker and more compact appearance. The mycelium does not invade the

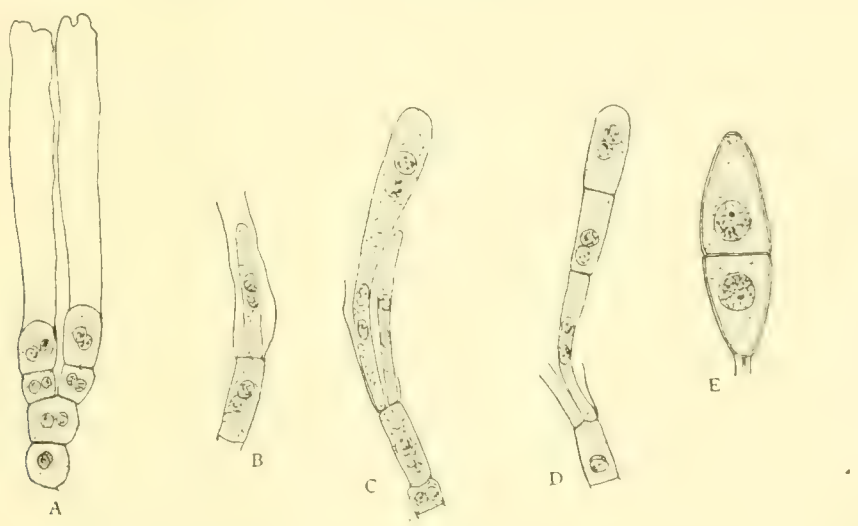



FIG. 5. *a*, pseudoparenchyma with buffer cells; *b*, 2-nucleated stage of the young teleutospore; *c*, 4-nucleated stage; *d*, 6-nucleated stage with cross walls; *e*, small spore after nuclear fusion.

vascular tissue even to the extent of penetrating the phloem of the stem. Both *G. transformans* and *G. fraternum* are capable of producing sori two or three years in succession, the latter may produce a sorus even after the leaf has apparently died. While haustoria are more numerous and attack the individual cells more vigorously in the case of the latter species, *G. transformans* seems in some way to be more destructive, as infected leaves more frequently die after maturity of the first sorus. Of the two species, *G. fraternum* is clearly the more nearly related to *G. biseptatum*, both from the nature of their teleutospores and the similarity of the aecidia in the two species. If the mycelium of *G. fraternum* is ever able to push in beyond the large cells surrounding a vein and get into the central cylinder of the stem, therefore nearer the cambium, we should look for a stimulus such as

might lead to the formation of a greater amount of wood tissue such as we find in the burl of *G. biseptatum*. *G. fraternum* has almost constantly 2-celled teleutospores, 3-celled spores are exceedingly rare. In *G. biseptatum* 3- and 4-celled spores predominate. I should be highly gratified to learn that the change in environment from the leaf to the stem, or more exactly from cortex to phloem, by the fungus could bring about such a decided change in the structure of its spores.

## EXPLANATION OF PLATE I

*Gymnosporangium transformans*

Stages in the Germination of the Aecidiospores. × 750

FIG. 1. A binucleated spore.

FIG. 2. The germ tube has pushed out, the nuclei are still within the spore and do not show appreciable change in form.

FIG. 3. One nucleus is crowding through the germ pore, the other lies beneath. The "pouch" is formed just back of the tip of the germ tube.

FIG. 4. Both nuclei have escaped from the spore and lie just outside of the germ pore.

FIG. 5. Two nuclei lie in the expanded portion of the germ tube.

FIG. 6. Four nuclei are plainly visible in the "pouch." The germ tube has not begun the second stage of its growth.

FIG. 7. Tip end of fully developed germ tube showing four nuclei in a row.

FIGS. 8 and 9. Other fully developed germ tubes showing a more pronounced type of branching.

FIG. 10. The germ tube has made about the maximum growth of which it is capable under artificial conditions, a cross wall cuts off the main portion of the granular cytoplasm at the forward end of the germ tube.

DODGE: GYMNOSPORANGIUM TRANSFORMANS

# INTERCROSSES BETWEEN SELF-STERILE PLANTS

E. M. EAST

*Bussey Institution, Harvard University*

The fact that self-fertilization is practically impossible in certain hermaphroditic plants, although both the pollen and the ovules are functional in crosses, has been known since the time of Kölreuter (1760–1765). The oddity of the phenomenon has been a lure for almost every hybridist from that time forward. As in the case of most other genetical problems, however, our knowledge of its cause and meaning remained in *status quo* from the time of Darwin until Mendelian days. Indeed when the writer began his investigations on the subject in 1910, the only considerable post-Darwinian work had been done by a zoologist (Morgan, 1904) on the self-sterile ascidian, *Ciona intestinalis*. Since 1910 botanical papers have appeared by Correns (1912), Compton (1913) and Stout (1916), but these investigations will not be discussed here, as it is proposed to treat in this paper only certain phases of the work carried on by the author and his associates[1] during the past seven years, leaving critical review for another place. For our purpose it seems essential only to present a hasty sketch of the subject as left by Darwin.

In addition to the utilization of most of the previous and the contemporaneous work, Darwin (1876) carried out several investigations of his own on the five self-sterile species, *Eschscholtzia californica*, *Abutilon darwinii*, *Senecio cruentus*, *Reseda odorata* and *Reseda lutea*.

Darwin's first important result was that the expression of self-sterility in *Eschscholtzia californica* and *Abutilon darwinii* was influenced by changes in external conditions. Six generations of *Eschscholtzia californica* had been found to be completely sterile in southern Brazil by Fritz Müller (1868, 1873). As English plants were self-fertile, Darwin obtained from Müller seed of Brazilian plants of known self-sterility. The plants which they produced in England, while not wholly self-fertile, tended toward self-fertility, which fact Darwin attributed to the lower English temperature. A second generation of seedlings proved to be still more self-fertile. Conversely, seed of English stock was somewhat self-sterile the first season and one plant

[1] The author desires to make grateful acknowledgment to Dr. O. E. White and Dr. J. B. Park for their painstaking aid in this work. Without it, the numerous experiments undertaken could not have been completed.

wholly self-sterile the second season, when grown in Brazil. One may assume, I think, arguing from data of similar character, that this progressive result was not due to actual inheritance of an acquired character but rather to the fact that the first generation in each case passed a portion of its life cycle in the original environment.

Similar results were obtained in the case of *Abutilon darwinii*, which though self-sterile in its native Brazil, *became moderately self-fertile late in the first flowering season in Darwin's greenhouse.*

Darwin made more detailed experiments on *Senecio cruentus*, *Reseda odorata* and *Reseda lutea* and found, as he believed, that each plant though self-sterile was cross-fertile with every other plant. His pollination experiments with *Senecio cruentus* and *Reseda lutea* were so inadequate that they may be omitted from consideration; it was really his experiments on *Reseda odorata* that were thought to establish the fact of complete cross-fertility.

DARWIN'S EXPERIMENTS ON *Reseda odorata* IN 1868

| Female Parents \ Male Parents | *A* | *B* | *C* | *D* | *E* | *F* | *G* |
|---|---|---|---|---|---|---|---|
| *A* | S. | F. | F. | | | | |
| *B* | F. | S. | F. | F. | | | |
| *C* | F. | F. | S. | F. | F. | | |
| *D* | F. | F. | F. | S. | F. | | |
| *E* | F. | | F. | F. | S. | | |
| *F* | | | | | | S. | |
| *G* | | | | | | | S. |

Only sixteen cross matings were made, however, and this is not sufficient to prove the point, as is shown by one of our own experiments, where 131 cross-matings were made with only 4 cases of cross-sterility. From the fertile cross-pollinations Darwin raised four plants in 1869. Three of these proved to be self-fertile and one self-sterile. Six more plants were grown in 1870. Of these, two were almost self-sterile and four were almost completely self-fertile. The former produced altogether five seeds from self-pollinations, and the resulting plants proved to be self-sterile like their parents. These varied results Darwin attributed to a difference in inherited sexual constitution, but it seems to me that this conclusion should be questioned. Our own resu lts have proved conclusively that toward the

very last of the flowering season[2] self-sterile plants may sometimes become somewhat self-fertile.

Darwin's (1876, p. 346) general conclusions are as follows:

"Finally, the most interesting point in regard to self-sterile plants is the evidence which they afford of the advantage, or rather the necessity, of some degree or kind of differentiation in the sexual elements, in order that they should unite and give birth to a new being. It was ascertained that the five plants of *Reseda odorata* which were selected by chance could be perfectly fertilised by pollen taken from any one of them, but not by their own pollen; and a few additional trials were made with some other individuals, which I have not thought worth recording. So again, Hildebrand and Fritz Müller frequently speak of self-sterile plants being fertile with the pollen of any other individual; and if there had been any exception to the rule, these could hardly have escaped their observation and my own. We may therefore confidently assert that a self-sterile plant can be fertilised by the pollen of any one out of a thousand or ten thousand individuals of the same species, but not by its own. Now it is obviously impossible that the sexual organs and elements of every individual can have been specialised with respect to every other individual. But there is no difficulty in believing that the sexual elements of each differ slightly in the same diversified manner as do their external characters; and it has often been remarked that no two individuals are absolutely alike. Therefore we can hardly avoid the conclusion that differences of an analogous and indefinite nature in the reproductive system are sufficient to excite the mutual action of the sexual elements, and that unless there be such differentiation fertility fails."

One cannot but admire these inductions Darwin has so cleverly drawn from such meager data, nevertheless one cannot accept them today just as they stand. The reasons for this statement will be seen more clearly when our own data have been presented, but a brief can be submitted with only the support of the work known to Darwin.

In the first place, the seemingly contradictory results that were obtained in the experiments on *Reseda odorata* are not necessarily confusing. As reported, self-sterile plants produced varying ratios of self-sterile and self-fertile plants. Unfortunately, the progeny of the self-fertile plants was not followed. If it has been, the problem might have been more easily solved, for, in all probability, the daughter plants would have been self-sterile. It is my own belief, however, that the answer can be read in the casual remarks dropped by Darwin in the midst of his careful descriptions, remarks to which he paid little attention. Darwin found that both *Eschscholtzia californica* and *Abutilon darwinii*, though self-sterile in Brazil tended to become self-fertile in England,—especially late in the flowering season. Now

[2] Cf. Darwin's observation on *Abutilon darwinii*.

these facts together with that mentioned above regarding the inconstancy of the results obtained from planting the seed of self-sterile plants, may be interpreted by the assumption that he was dealing entirely with fluctuations in all of the five species investigated. These species genetically were wholly self-sterile. The tendency toward self-fertility was due to conditions. In other words, these plants genetically self-sterile needed conditions conducive to a fine healthy growth to bring out their self-sterility. In the lower temperature of England, at a time of decline (the last of the flowering season), they became phenotypically somewhat self-fertile. In the light of my own experiences, I believe we can reconstruct a picture of Darwin's experiments on *Reseda odorata* with considerable confidence. He isolated the plants that he desired to test under nets; then came pressure of other work, and the data were not collected until the plants had ceased flowering. At that time capsules were found beneath the nets, and this seemed to prove at least a partial self-fertility. But instead of this procedure, suppose that successive self-pollinations had been made throughout the season. The presumption is that the plants would have been declared to be self-sterile with the same remark added which he jotted down in the case of *Abutilon darwinii*, viz., they "became moderately self-fertile late in their flowering season."

Again, Darwin found no cross-sterility in the plants tested, and concluded that a self-sterile plant can be fertilized with the pollen of any one of a thousand or ten thousand individuals of the same species. Such a conclusion was less cautious than was Darwin's wont for it was made from a total personal experience of some twenty-odd crossmatings only, unless his records are extremely incomplete. Indeed this conclusion must have been somewhat of a surprise to himself since he states that "it is obvious impossible that the sexual organs and elements of every individual can have been specialized with respect to every other individual." He surmounted this difficulty by assuming that the sexual elements of each plant differ slightly in the same manner as their external characteristics, and that this slight difference is sufficient to excite the mutual action of the sex elements necessary in order to have fertilization ensue. The kernel in this conclusion, that differences in the reproductive systems of two self-sterile plants are necessary in order to promote cross-fertilization, is so similar to that to which the writer has been forced after seven years of rather intensive work as to be uncanny, for it seems to have been reached in spite of rather than because of the data at hand. This feeling of surprise at Darwin's clairvoyancy may seem affected, since he was usually in advance of his time, but it is a fact perhaps worth mentioning as a confession of omission that the writer reached his con-

clusions as the outgrowth of work on heterozygosis and did not refer to Darwin's view until recently. Be this as it may, a short comparison of Darwin's main induction with the facts from which it came will, I think, show a real reason for wonderment. He believed in universal cross-fertility of self-sterile plants, his basis being the small number of cross-fertilizations made by Hildebrand, Müller and himself; although Robertson Munro (1868), with whose work he was familiar, had found cross-sterility in *Passiflora alata*, and even the works of Hildebrand and Müller as published leave the matter in doubt. Now how much more reasonable the general induction mentioned above seems if one assumes (1) that self-sterile plants breed true for self-sterility but may show a slight degree of self-fertility as a fluctuation under certain conditions, (2) that a variable but limited number of germinal "factors" influence the success of matings, cross-fertilization being possible only when two plants differ in these effective factors, and (3) that when two plants have the same effective factorial composition, cross-sterility of the same type as self-sterility exists. This is what we believe our own work has shown, as we shall try to demonstrate.

Emphasis must first be laid upon the fact that the behavior of self-sterile plants among themselves and the relation between self-fertile and self-sterile plants are distinct problems. Compton (1913) found the relation between self-fertile and self-sterile plants of *Reseda odorata* to be that of a simple Mendelian monohybrid with self-fertility dominant. The same relation appears to hold in crosses between the self-fertile species *Nicotiana langsdorffii* and the two self-sterile species with which our work has been done, *Nicotiana forgetiana* and *Nicotiana alata*. There is some single differential between self-fertility and self-sterility. Given the proper composition a plant breeds true for self-sterility. The behavior of self-sterile plants among themselves therefore must be considered separately.

Our work, as stated before, has been done with the two self-sterile species, *Nicotiana forgetiana* and *Nicotiana alata*, and largely with crosses between these species. Both of these species are affected in their manifestation of self-sterility by certain environmental changes, *Nicotiana alata* much more than *Nicotiana forgetiana*. Self-sterility is determined by the inheritance received, but it can develop fully only under environmental conditions which promote a normal healthy growth, and during the period of intense flowering. Toward the end of the flowering period, especially under conditions adverse to vegetative growth, self-sterility sometimes shows a marked and rather sudden decline. A few seeds, or even a well-developed seed capsule may then be obtained. This is not a common occurrence; indeed, it

is rare, but it is a possibility. Three cases of seed production out of over three hundred plants tested have been observed in *Nicotiana forgetiana*. A considerably higher percentage of fertility has been marked in *Nicotiana alata*. Self-sterility can be restored in such plants, however, if they are allowed to go through a period of rest and are then, by proper treatment, brought into vigorous flower again.

This is not the whole evidence that this occasional end-season fertility is a pseudo-fertility brought about by external conditions—a fluctuation. Three generations of *Nicotiana alata* plants have been grown from selfed seed produced by end-season fertility without the occurrence of a single plant which behaved in every way like a truly self-fertile individual. This phenomenon, therefore, while teaching us to test self-sterility only during the main part of the flowering season, has shown that there is no reason why fusion between gametes produced by a self-sterile plant may not occur provided the male generative nucleus enters the embryo sac. Such unions may take place without affecting the self-sterility of the progeny.

What is then the difference in behavior that makes a cross-pollination effect fertilization while a self-pollination produces nothing? What occurs is this: After a self-pollination the pollen grains germinate and the tubes pass down the style at such a slow even rate that they reach only about half way to the ovary before the flower wilts and falls off; while the pollen tubes after a cross-pollination, though starting at the same rate as the others, grow faster and faster until fertilization is effected in four days or less. The curve of distance traversed plotted against time is in the case of the self-pollination nearly a straight line, while in the case of the cross-pollination it simulates that of an autocatalytic reaction.

From these facts it seems reasonable to suppose that the secretions in the style offer a stimulus to pollen tubes from other plants rather than an impediment to the development of tubes from pollen of the same plant. And we believe that this stimulus is in some way caused by certain effective differences in the factorial composition characterizing two compatible plants and that if two plants do not have these effective differences in factorial composition they are by the same token cross-sterile with each other. It is clear that this assumption presumes that the pollen grains matured by a given plant behave as if they are sporophytic as regards that part of their constitution that affects self-sterility and cross-sterility. The pollen grains of any plant may carry many different hereditary factors, they may even carry several different factors which function in controlling the success or failure of particular cross-matings in the next generation, but in their own action on the stigmas of other plants they behave

as if each carried the composition of the mother plant from which it came. In other words, as far as its action in fertilization is concerned, a pollen grain partakes of the character of its mother plant and is like its sisters; as far as the hereditary characters carried on to the next generation are concerned, sister pollen grains may differ both from their mother and from each other.

A part of our evidence on these points we shall present. For further details the reader is referred to a forthcoming paper in Genetics.[3]

The first experiment to which attention is called is an inbreeding experiment performed on a cross between *Nicotiana forgetiana* and *Nicotiana alata*. If sister plants are mated in successive generations after an original mating Aa × Aa, by Mendelian recombination there results a gradual approach to 1/2 AA, 1/2 aa and 0 Aa. Expectation of homozygosis in successive matings is 1/2, 5/8, 11/16, 24/32 · · · 1 (Jennings, 1916). If, therefore, plants of like constitution as far as effective factors are concerned are cross-sterile with each other, cross-sterility should become more and more apparent in generations succeeding $F_2$. To test this possibility, a comparatively small number of cross-matings was made on the $F_2$, $F_3$, $F_4$ and $F_5$ generations. In the $F_2$ generation, out of 131 intercrosses on 20 plants only 4 were unsuccessful. The percentage of unsuccessful matings increased from this time on, until in the $F_5$ generation about 21 percent of the cross-matings tried on 20 plants were impossible to make.

In this experiment as well as in all others, results showed that reciprocal crosses were alike in their compatibility. If two plants were fertile together, they were fertile reciprocally; if two plants were incompatible, they were incompatible reciprocally. This is proof of the sporophytic behavior of the factors affecting the behavior of self-sterile plants.

The two crosses to be described next are reciprocals made with the same two individuals. Made with *Nicotiana alata* and *Nicotiana forgetiana* as parents, they are in a sense repetitions of the cross just described, but it is hardly probable that they duplicate it. Both of these species must consist of plants which differ among themselves in the factors which affect self-sterility, hence any crosses in which different individuals are used may show different results.

All of the individuals resulting from this cross were grown in a greenhouse as potted plants. The $F_1$ generation came into blossom during the latter part of the winter. Conditions were extraordinarily favorable for growth and the pollinations were all made while the plants were vigorous, hence scarcely any trouble arose over classification of the results through end-season pseudo-fertility.

[3] This paper has since appeared. See "Studies on Self-sterility I. The Behavior of Self-sterile Plants." Genetics 2: 505–609. 1917.

Our study was made on a population of 53 plants. Pedigree numbers from 0 to 39 inclusive represent the cross *N. alata* × *N. forgetiana;* pedigree numbers 40 to 52 inclusive represent cross *N. forgetiana* × *N. alata.*

Each plant was selfed one or more times, and all proved absolutely self-sterile. Further *each plant* was *back-crossed* with pollen from a single plant of each of the parent species *with complete success in every case.* The plants used in this case were not the individuals that entered into the cross, however, for unfortunately these were not available.

TABLE I

RESULT OF MATINGS ON $F_1$ PLANTS 0 TO 39

*N. alata* × *N. forgetiana* and on Plants 41 to 52 *N. forgetiana* × *N. alata*

| Ped. No. | Fertile with Ped. No. | Sterile with Ped. No. |
|---|---|---|
| 0 | 44, 46 | 22, 34, 38, 49 |
| 1 | 2, 3, 4, 6, 41 | 8 |
| 2 | 4, 18, 41, 44, 52 | 9, 22, 23 |
| 3 | 2, 9, 14, 23, 29 | 4, 6, 18, 41, 46 |
| 4 | 2, 9, 10, 44 | 18 |
| 5 | 2, 3, 6, 9, 10, 18, 46 | 8, 44 |
| 6 | 5, 10, 43, 44 | 3, 4, 18, 40 |
| 7 | 2, 13, 22, 44 | 18, 46 |
| 8 | 6, 9, 10, 39, 40, 46 | 5, 44 |
| 9 | 3, 18, 44, 52 | 2, 10, 23, 37, 48 |
| 10 | 4, 6, 18, 40, 44 | 2, 23, 24, 27, 34, 48 |
| 11 | 2, 8, 12, 15, 34, 44, 46 | |
| 12 | 9, 16, 22, 43 | 6, 18, 46, 52 |
| 13 | 3, 8, 18, 44, 46 | 2, 9, 15, 21, 34 |
| 14 | 18, 20, 43 | 10, 34 |
| 15 | 1, 3, 16, 17, 18, 20 | 9, 13, 14, 23, 44 |
| 16 | 13, 14, 18, 25, 43, 46 | 17, 29 |
| 17 | 14, 18, 19, 20, 22, 30 | 16, 26, 44 |
| 18 | 2, 9, 21, 23, 28, 34, 36, 44 | 3, 46 |
| 19 | 17, 22, 28, 34, 44 | 18 |
| 20 | 2, 8, 9, 16, 18, 21, 22, 26, 36, 40, 44 | 43 |
| 21 | 4, 12, 16, 18, 46 | 2, 9, 22, 25, 27, 37 |
| 22 | 12, 42, 44 | 14, 23, 24, 36, 48 |
| 23 | 41 | 9, 10, 37, 48 |
| 24 | 3, 6, 20, 26, 28, 44 | 10, 22, 23, 30, 37 |
| 25 | 8, 33, 44, 46 | 2, 9, 23, 27 |
| 26 | 9, 18, 22, 23, 25, 40, 48 | 28, 29, 44 |
| 27 | 3, 18, 32, 44, 46 | 2, 9, 30, 34, 48 |
| 28 | 2, 3, 23, 27, 39, 46 | 8, 26, 29, 44 |
| 29 | 2, 14, 18, 22, 23, 24, 25, 30, 34, 37, 41, 46 | 5, 26, 28, 31, 44 |
| 30 | 8, 29, 33, 44, 45, 46 | 9, 21, 22, 27 |
| 31 | 22, 32, 52 | 8, 29, 36, 44 |
| 32 | 9, 21, 23, 29, 30, 34, 43, 44 | 18, 33, 46 |
| 33 | 8, 16, 23, 31, 46 | 18, 32 |
| 34 | 28, 41, 44, 46 | 10, 23, 24, 37 |
| 35 | 3, 9, 18, 21, 27, 30, 34, 37, 42 | 8 |
| 36 | 8, 33, 44, 46 | 10, 23 |
| 37 | 39, 42, 43, 44, 46 | 9, 10, 22, 23, 34, 38 |

| | | |
|---|---|---|
| 38 | 28, 35, 39, 42, 43, 46 | 34, 37, 47 |
| 39 | 9, 44 | 18, 40, 42 |
| 40 | 22, 43, 44, 47, 49 | 6, 33, 46 |
| 41 | 10, 37, 44, 48 | 33, 40, 46 |
| 42 | 20, 44 | 39, 41, 45 |
| 43 | 5, 27, 33, 38, 39, 40, 42, 44, 46, 51 | |
| 44 | 10, 14, 23, 34, 45 | |
| 45 | 18, 44, 48 | 46, 52 |
| 46 | 10, 22, 37, 44, 51 | 52 |
| 47 | 20, 42, 44, 45, 46, 51, 52 | 38 |
| 48 | 40, 41, 43, 46 | 10, 23, 24, 27, 34 |
| 49 | 42, 44, 45 | 0, 9, 27, 34, 47 |
| 50 | 18, 39, 51, 52 | 9, 27, 37 |
| 51 | 9, 18, 23, 39, 45, 46, 50 | 8, 29 |
| 52 | 10, 23, 29, 37, 51 | 3, 4, 6, 18, 41, 45, 46 |

The numerous cross-matings made are shown in Table 1. There were 103 reciprocal matings. Of these 100 gave duplicate results, 39 pairs being fertile and 61 sterile. The three which did not check are:

$2 \times 3$, sterile, 1 pollination
$3 \times 2$, fertile, 1 pollination
} classed as fertile,

$6 \times 52$, fertile, 1 pollination
$52 \times 6$, sterile, 1 pollination
} classed as sterile,

$37 \times 21$, fertile, 1 pollination
$21 \times 37$, sterile, 1 pollination
} classed as sterile.

Since but one pollination was made in each of these cases we have made our decision as to fertility or sterility by a consideration of the circumstantial evidence. The behavior of these plants in other crosses shows conclusively that 3 should be fertile with 2, 6 sterile with 52, and 21 sterile with 37. They have been classed accordingly. That this grouping is correct is further shown by the fact that the mating $3 \times 2$ (classed fertile) was made at the height of the flowering season, while the matings $6 \times 52$ and $37 \times 21$ (classed sterile) were respectively the last and next to the last matings made on those plants.

In spite of the fact that plants 0–39 are from cross *N. alata* × *N. forgetiana*, and plants 40–52 are from cross *N. forgetiana* × *N. alata*, they behave as one family in intercrosses. The entire population can be grouped into 6 classes in which there is interclass fertility and intraclass sterility. The following explanation may be necessary to make it clear just how Table II was obtained from Table I. Table I shows all of the matings, but in the form given it is not easy to see at a glance every combination in which a particular plant was used, both as male and as female. It was necessary, therefore, to make a new table, in which the pedigree numbers in the column at the left were tabled as males, and the pedigree numbers in the columns headed "Fertile matings" and "Sterile matings" were tabled as females.

Thus plant 2, used as a female, was fertile with pollen from plants 4, 18, 41, 44 and 52, and sterile with plants 9, 22 and 23; but pollen from plant 2 was fertile on plants 1, 3, 4, 5, 7, 11, 18, 20, 28 and 29, and sterile on plants 9, 10, 13, 25 and 27. It is clear, therefore, that instead of the 8 matings on plant 2 that Table I appears to show, there are really 21, the 3 reciprocals of course being counted but once.

These tables were combined for analysis. In the interest of economy of space only one is shown, however, since the second can easily be made from the first.

The four exceptions in this huge set of matings are in reality negligible. Matings 15 × 44 and 31 × 36 were sterile, though they do not belong to the same class. Plant 15 was sterile to 4 plants of Class *A* and fertile to 2 plants of Class *B*, 3 plants of Class *C*, and to the isolated individuals forming classes *D* and *F*. It is unquestionably a member of Class *A*. Plant 44 was sterile to 7 individuals in Class *C* and fertile to 17 plants of Class *A*, 12 plants of Class *B* and to the singletons forming classes *D*, *E* and *F*. This evidence places it unmistakably as a member of Class *C*. Plant 31 is also a member of Class *C* as evidenced by 3 sterile matings within that class and by fertile matings with 1 plant of Class *A* and 3 plants of Class *B*. Plant 36 is like plant 15 thrown into Class *A* by its sterility with 3 others of that class, and by its fertility with 3 individuals of Class *B*, with 2 of Class *C*, and with the lone plant of Class *D*. In view of this evidence and the fact that in these two matings but one pollination was made in each case, they are much more likely to be errors of record or of technique than true exceptions to our classification.

The other two exceptions, matings 45 × 18 and 33 × 46, were fertile where from the evidence of numerous other matings they should have been sterile. Here again but one pollination was made in each case; and, coincidence though it may be, *each pollination was the last mating made on that particular plant.* What is more probable than that this is a pseudo-fertility appearing during the wane of the flowering season of the two mother plants, No. 45 and No. 33?

Six groups appear in Table II, but there is proof of the existence of only five. Groups *A*, *B*, *C*, *D* and *E* are definitely established. Plant 11, on the other hand, is an isolated individual rather than a class. It does not belong to groups *A*, *B* or *C*; but unfortunately it was not crossed either with Class *D* (plant 20) or with Class *E* (plant 43), hence one cannot say that it does not fall into one or the other of these two classes.

In the three large groups the distribution of individuals is 22, 16 and 12. About all that can be said about the type of this distribution is that the classes are not of equal size. On the other hand, it is

interesting to note that the plants of both cross No. 2 and cross No. 3 fell into the three groups as if they were samples of the same population. There were 40 plants of Cross No. 1, and 13 plants of the

TABLE II

PLANTS OF $F_1$ GENERATION OF RECIPROCAL CROSS BETWEEN *N. forgetiana* AND *N. alata*, GROUPED IN ACCORDANCE WITH THEIR BEHAVIOR IN INTERCROSSES

Plants 0–39 are products of the cross; plants 40–52 are products of its reciprocal

| Group | Ped. No. | Cases Fertile in Group | | | | | | Cases Sterile in Group | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | *A* | *B* | *C* | *D* | *E* | *F* | *A* | *B* | *C* | *D* | *E* | *F* |
| *A*..... | 0 | 0 | 1 | 1 | – | – | – | 4 | 0 | 0 | – | – | – |
| | 2 | 0 | 6 | 5 | 1 | – | 1 | 8 | 0 | 0 | 0 | – | 0 |
| | 9 | 0 | 7 | 6 | 1 | – | – | 13 | 0 | 0 | 0 | – | – |
| | 10 | 0 | 7 | 3 | – | – | – | 10 | 0 | 0 | – | – | – |
| | 13 | 0 | 4 | 3 | – | – | – | 5 | 0 | 0 | – | – | – |
| | 14 | 0 | 2 | 4 | 1 | 1 | – | 4 | 0 | 0 | 0 | 0 | – |
| | 15 | 0 | 2 | 3 | 1 | – | 1 | 4 | 0 | 1 | 0 | – | 0 |
| | 21 | 0 | 5 | 2 | 1 | – | – | 8 | 0 | 0 | 0 | – | – |
| | 22 | 0 | 6 | 5 | 1 | – | – | 9 | 0 | 0 | 0 | – | – |
| | 23 | 0 | 6 | 5 | – | – | – | 11 | 0 | 0 | – | – | – |
| | 24 | 0 | 2 | 4 | 1 | – | – | 7 | 0 | 0 | 0 | – | – |
| | 25 | 0 | 2 | 5 | – | – | – | 5 | 0 | 0 | – | – | – |
| | 27 | 0 | 4 | 3 | – | 1 | – | 10 | 0 | 0 | – | 0 | – |
| | 30 | 0 | 4 | 5 | – | – | – | 5 | 0 | 0 | – | – | – |
| | 34 | 0 | 5 | 4 | – | – | 1 | 11 | 0 | 0 | – | – | 0 |
| | 36 | 0 | 3 | 2 | 1 | – | – | 3 | 0 | 1 | 0 | – | – |
| | 37 | 0 | 5 | 3 | – | 1 | – | 9 | 0 | 0 | – | 0 | – |
| | 38 | 0 | 3 | 2 | – | 1 | – | 4 | 0 | 0 | – | 0 | – |
| | 47 | 0 | 5 | 2 | 1 | – | – | 2 | 0 | 0 | 0 | – | – |
| | 48 | 0 | 4 | 1 | – | 1 | – | 7 | 0 | 0 | – | 0 | – |
| | 49 | 0 | 3 | 1 | – | – | – | 5 | 0 | 0 | – | – | – |
| | 50 | 0 | 3 | 1 | – | – | – | 3 | 0 | 0 | – | – | – |
| *B*..... | 3 | 8 | 0 | 5 | – | – | – | 0 | 6 | 0 | – | – | – |
| | 4 | 4 | 0 | 2 | – | – | – | 0 | 4 | 0 | – | – | – |
| | 6 | 2 | 0 | 4 | – | 1 | – | 0 | 6 | 0 | – | 0 | – |
| | 7 | 3 | 0 | 1 | – | – | – | 0 | 2 | 0 | – | – | – |
| | 12 | 3 | 0 | 1 | – | 1 | 1 | 0 | 4 | 0 | – | 0 | 0 |
| | 18 | 12 | 1 | 9 | – | – | – | 0 | 11 | 0 | 0 | – | – |
| | 19 | 2 | 0 | 3 | – | – | – | 0 | 1 | 0 | – | – | – |
| | 32 | 6 | 0 | 3 | – | 1 | – | 0 | 3 | 0 | – | 0 | – |
| | 33 | 4 | 1 | 3 | 0 | 1 | – | 0 | 4 | 0 | – | 0 | – |
| | 39 | 4 | 0 | 4 | – | 1 | – | 0 | 3 | 0 | – | 0 | – |
| | 40 | 5 | 0 | 3 | 1 | 1 | – | 0 | 5 | 0 | 0 | 0 | – |
| | 41 | 6 | 0 | 3 | – | – | – | 0 | 6 | 0 | – | – | – |
| | 42 | 5 | 0 | 2 | 1 | 1 | – | 0 | 3 | 0 | 0 | 0 | – |
| | 45 | 4 | 1 | 2 | – | – | – | 0 | 3 | 0 | – | – | – |
| | 46 | 14 | 1 | 7 | – | 1 | 1 | 0 | 9 | 0 | – | 0 | 0 |
| | 52 | 7 | 0 | 3 | – | – | – | 0 | 8 | 0 | – | – | – |
| *C*..... | 1 | 2 | 4 | 0 | – | – | – | 0 | 0 | 1 | – | – | – |
| | 5 | 3 | 4 | 0 | – | 1 | – | 0 | 0 | 3 | – | 0 | – |
| | 8 | 6 | 5 | 0 | 1 | – | 1 | 0 | 0 | 7 | 0 | – | 0 |

TABLE II—*Continued*

| Group | Ped. No. | Cases Fertile in Group | | | | | | Cases Sterile in Group | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | *A* | *B* | *C* | *D* | *E* | *F* | *A* | *B* | *C* | *D* | *E* | *F* |
| *C*..... | 16 | 5 | 4 | 0 | 1 | 1 | – | 0 | 0 | 2 | 0 | 0 | – |
| | 17 | 4 | 2 | 0 | 1 | – | – | 0 | 0 | 3 | 0 | – | – |
| | 26 | 6 | 2 | 0 | 1 | – | – | 0 | 0 | 4 | 0 | – | – |
| | 28 | 6 | 5 | 0 | – | – | – | 0 | 0 | 4 | – | – | – |
| | 29 | 9 | 6 | 0 | – | – | – | 0 | 0 | 7 | – | – | – |
| | 31 | 1 | 3 | 0 | – | – | – | 1 | 0 | 3 | – | – | – |
| | 35 | 7 | 3 | 0 | – | – | – | 0 | 0 | 1 | – | – | – |
| | 44 | 17 | 12 | 0 | 1 | 1 | 1 | 1 | 0 | 7 | 0 | 0 | 0 |
| | 51 | 4 | 5 | 0 | – | 1 | – | 0 | 0 | 2 | – | 0 | – |
| *D*..... | 20 | 9 | 3 | 5 | 0 | 1 | – | 0 | 0 | 0 | 0 | 0 | – |
| *E*..... | 43 | 5 | 8 | 4 | 1 | 0 | – | 0 | 0 | 0 | 0 | 0 | – |
| *F*..... | 11 | 3 | 2 | 2 | – | – | 0 | 0 | 0 | 0 | – | – | 0 |

reciprocal, Cross No. 2. In the classes *A*, *B* and *C* the proportions were 18, 10, 10 and 4, 6, 2 respectively. This similar behavior of the progeny of reciprocals seems to us strong corroboratory evidence in favor of the conclusion that reciprocal crosses always behave in like manner as regards self-sterility.

The study on this family is but one of several that have been made but we believe that the data on it alone show unmistakably that the behavior of self-sterile plants in intercrosses is governed by a relatively small number of factors which act through pollen as if the pollen grain possessed the characters of the sporophyte from which it came, and that the gametes of plants having like constitutions as regards effective factors are incompatible in the sense that they do not make a normal pollen-tube growth and hence do not reach the ovary in time for fusion to occur. This interpretation shows both why plants are self-sterile and cross-sterile. It accords completely with the fact that a population of plants may be divided into groups on the basis of their mating proclivities and that each member of any group is cross-sterile with every other individual of that group although it is fertile with every individual of every other group.

These assumptions being true, it ought to be possible by continuous self-fertilization, utilizing end-season pseudo-fertility, to obtain ultimately a population in which every individual possesses the same effective self-sterility factors. In such a population all of the plants will not only be self-sterile, but will be cross-sterile. Such a population has been obtained.

## REFERENCES CITED

**Compton, R. H.** Phenomena and Problems of Self-sterility. New Phytologist **12**: 197–206. 1913.

**Correns, C.** Selbststerilität und Individualstoffe. Festschr. d. mat.-nat. Gesell. zur 84. Versamml. deutsch. Naturforscher u. Ärzte Münster i.W. pp. 1–32. 1912.

**Darwin, Chas.** Effects of Cross- and Self-fertilisation in the Vegetable Kingdom. Ed. 2, 1878. N. Y. D. Appleton. 1876.

**Hildebrand, F.** Bastardierungs Versuche an Orchideen. Bot. Ztg. **23**: 245–249. 1865.

—— Ueber die Nothwendigkeit der Insektenhilfe bei der Befruchtung von *Corydalis cava*. Jahrb. wiss. Bot. **5**: 359–363. 1866.

—— Ueber die Bestäubungsvorrichtungen bei den Fumariaceen. Jahrb. wiss. Bot. **7**: 423. 1869.

**Jennings, H. S.** The Numerical Results of Diverse Systems of Breeding. Genetics **1**: 53–89. 1916.

**Kölreuter, J. G.** Vorläufige Nachricht von einigen das Geschlecht der Pflanzen betreffenden Versuchen und Beobachtungen, nebst Fortsetzungen 1, 2 u. 3. Pp. 1–266. Ostwald's Klassiker, Nr. 41. Leipzig: Engelmann. 1761–6.

**Morgan, T. H.** Some Further Experiments on Self-fertilization in Ciona. Biol. Bull. **8**. 313–330. 1904.

**Müller, Fritz.** Notizen über die Geschlechtsverhältnisse brasilianischer Pflanzen. Bot. Ztg. **26**: 113–116. 1868.

—— Bestäubungsversuche an Abutilon-Arten. Jen. Ztschr. f. Naturwiss. **7**: 22–45, 441–450. 1873.

**Munro, Robertson.** On the Reproduction and Cross-fertilization of Passifloras. Bot. Soc. Edin. **9**: 399–402. 1868.

**Stout, A. B.** Self- and Cross-pollinations in *Cichorium intybus* with Reference to Sterility. Mem. N. Y. Bot. Gard. **6**: 333–454. 1916.

# BINARY FISSION AND SURFACE TENSION IN THE DEVELOPMENT OF THE COLONY IN VOLVOX

R. A. HARPER

*Columbia University*

In *Volvox* we have an incipient metaphyte with a many-celled body of definitely organized form and the fundamental differentiation of soma and germ cells fully established. Klein's ('89, '90) argument that *Volvox* differs from true metaphytes in that the differentiation of the germ cells does not take place until after cell division is completed is not very illuminating. The germ cells do not appear in *Oedogonium* until a considerable series of undifferentiated cells have been formed. Falkenberg's comparison of the entire colony to a zoosporangium also overlooks the very important fact that in the development of the *Volvox* colony growth regularly alternates with cell division (at least after the first few divisions) just as it does in the development of the soma of one of the higher metaphytes. *Volvox* is frequently referred to as one of the best known algae. There is general agreement as to the order of cell divisions in the formation of the colonies, both for the egg and the asexual germ cells. The literature has been frequently summarized.

To proceed further with the study of *Volvox* from the standpoint of evolution and morphogenesis, we may compare it with such a simple coenobe as *Gonium*. In addition to their more obvious structural characteristics there are two essential differences between the colonies in such forms as *Gonium* and *Volvox*. First, the adhesion between the daughter cells is much more firm in the latter. In *Gonium*, as all observers testify, the adult colonies break up into their component cells with the greatest readiness. I have figured such broken-up colonies ('12, Pl. V, Fig. 23). Slight pressure, change in the chemical composition of the medium in which they are, etc., lead to almost explosive separations. One marked difficulty in getting good photographs of the colonies is due to their tendency to go to pieces. On the other hand, *Volvox* shows almost no tendency to separate into its component cells. The colonies may be crushed into formless masses without isolating a single cell and I know of no chemical or other stimulus which will cause their cells to fly apart as do those of *Gonium*.

The second difference lies in the very fundamental fact that, as noted, in *Volvox* the germ cell grows to relatively large size before dividing and the daughter cells grow in size between the successive cell divisions. This is a very long step toward the full metaphytic habit in ontogeny. It marks a return to the habit of the simple protophyte like the bacteria and the appearance of a new point of departure in the development of the morphogenesis of a metaphytic plant body out of the primitive habit of reproduction by swarmspores which is seen in *Chlamydomonas* and *Sphaerella*. In these protophytes, the cell having reached maturity forms from four to eight swarmspores by rather rapidly succeeding divisions of the mother cell. They escape by breaking of the mother cell wall and then as free individuals proceed to grow to the size of the parent.

Swarmspore formation in *Chlamydomonas* and *Sphaerella* is a step beyond the conditions in *Euglena*, for example, where in ordinary reproduction each cell division is followed at once by the individualization of the daughter cells and their independence as separate organisms. In these particulars we may distinguish three steps in the evolution of the metaphyte from the typical protophyte.

1. Cell division, in simple, direct alternation with growth, reproduction and individualization, practically simultaneous and identical processes. *Euglena.*
2. Cell divisions at unequal intervals, reproduction multiple and in alternation with growth. Individualization delayed. *Chlamydomonas, Sphaerella.*
3. Cell division and growth in direct alternation, reproduction multiple and individualization delayed by intercalation of a true embryonic period. *Volvox.*

In *Volvox* individualization is already in essence the complex process of differentiation and maturing which we find in the highest plants and animals. In *Gonium* individualization of the daughter colony, as I have shown in a former paper ('12), is accompanied merely by certain gliding movements of the cells upon each other by which an approximation to a least surface configuration is achieved so far as is possible for sixteen ovoid cells arranged in a flat plate.

In *Volvox*, with the retention of multiple or colony reproduction as in *Sphaerella*, we have growth intercalated again between each successive cell division and also a specialization in function between germ and somatic cells. Complete individualization is delayed till the colony has become very many-celled. What may be called a pseudo-growth comparable to the elongation of the cells just back of the root tip by absorption of water and the formation of large central vacuoles is also represented in *Volvox* by the formation from the cell

walls, as Meyer has most fully described, of the large masses of slime by which the protoplasts in the adult colony are surrounded. This slime, about whose nature Cohn, Klebs, Blochmann, and others have differed so widely, is, as is now generally recognized, the gelatinized cell wall comparable to the secondary thickenings in collenchymatous tissues through which extend the broad strands which provide for the again much disputed intercellular protoplasmic connections which are so conspicuous in the adult colonies.

The firm adhesion of the daughter cells to each other and the re-establishment of the primitive cell division-growth rhythm are two further conditions to be reckoned with in the development of the colony of *Volvox* as compared with that of *Gonium*.

We may turn now to the morphogenetic processes involved in the reproduction of *Volvox*. Braun ('75) first clearly recognized the "division by the wheel-forming type" in *Eudorina* as distinguished from the ordinary successive bipartitions at right angles in *Palmella*, etc. Braun refers the readjustments of rounding up and rearrangement of the cells in forming the globular colony to the pressure of the developing slime envelopes.

It has not been sufficiently emphasized that in the two-cell stage and in the four-cell stage, as in the cleavage of the animal egg, the halves and the quadrants respectively will tend by surface tension to round up and give us a plate-shaped instead of a globular mass. In *Eudorina* Goebel shows that the four cells tend to round up and are shortened. He further represents them as tending to remain at one end of the mother-cell cavity and to adhere to the surface of the mother-cell wall. This leads to a divergence of their major axes and ('82, p. 36, Fig. 17) gives already at this stage a polar opening. Overton ('89, Taf. II, Fig. 10, *a*, *b*, *c*) figures evidence of this divergence of the four cells and it has been observed by others. The third division by the wheel type, or radial type, gives us with the rounding up of the cells a disk consisting of four interior and four peripheral cells alternating with them, the familiar cross figure. The four inner cells may appear much larger and are commonly so figured.

Overton ('89, Taf. II, Fig. 12, *a* and *b*) has shown very clearly that the apparent relative size of the central and peripheral cells varies with the level at which they are observed. The peripheral cells have slipped out of the plane of the central four so that the group of eight is already markedly concave. Two factors are primarily concerned in this displacement. First, the fact that we have by binary fission in two planes at right angles a group of eight rounded bodies which can form no stable least surface configuration in one plane and, second, the disk-shaped group formed by the rounding

up of the eight cells by surface tension tends to conform to the shape of the cavity of the mother cell. The whole is an expression of the incompatibility of the principles of surface tension and binary fission complicated still further by the rather firm adhesion of the cells to each other. If division had produced seven instead of eight cells and if they were free to adjust their interrelations in accord with their capacity to achieve a position in which their pressure relations were as nearly as possible mutually compensatory, we might have the typical least surface group of one surrounded by six in one plane. If ten cells were produced by division and if, as in *Hydrodictyon*, the rounded form of the mother cell were a dominating factor we might get one cell surrounded by five in the form of a saucer conforming to the curved surface of the mother cell. A further series of five added on the margin of the saucer and the figure could be closed by the remaining cell. If the eight cells produced by binary fission were free as in *Pediastrum*, we might get a group like the typical eight-celled colony of *P. Boryanum* with two inversely bilaterally symmetrically placed central cells and two groups of three peripheral cells also inversely bilaterally symmetrically placed with reference to each other ('16). Pressure of the mother cell might make the group slightly concave.

With eight cells produced by bipartition from four strongly adherent mother cells and themselves rather firmly adherent the familiar concave cross figure is the best approximation to a least surface configuration.

I have noted that in *Volvox* there is growth of the daughter cells intercalated between the divisions. This is very slight at first. In the early stages, as has been generally noted, the mass of the young colony seems little larger than that of the mother cell. In the preparation for the third division, however, there is a marked elongation of the four cells.

In the two-celled stage the halves appear symmetrical, or one cell may be slightly oblique (Fig. 1, Pl. II). In the four-celled stage the sectors at first appear quite symmetrical and uniform in appearance (Figs. 2, 3, Pl. II) but with the preparation for the third division a characteristic change in the form of the cells is observed. This growth period intercalated between the cell divisions is an essentially differentiating metaphytic character and makes possible in *Volvox* as in higher types the formation of the indeterminately large and many-celled colony as contrasted with the fewer-celled colonies of *Gonium*, *Pediastrum*, etc., in which the cell-division stages are sharply separated from the cell-growth stages. The growth in the four-celled stage of *Volvox* is quite specific in that it is not a mere swelling of the cell in

all its dimensions. It results rather in a characteristic elongation in one axis of the cell, the axes of elongation of the four cells tending to be tangential to the general outline of the four-celled group. Klein figures this elongation of the cells very clearly for *Eudorina* in the four- and again in the eight-celled stage ('88, Taf. VI, Fig. 61, 63). Overton shows it more crudely ('89, Taf. II, Fig. 10) and I have been able to photograph it for one of the four cells (Fig. 4, Pl. II). It may take place successively rather than simultaneously in the four cells and apparently proceeds in either direction around the group. Bütschli's figure ('83, Taf. XIV, 1 g.) shows rather crudely the resulting arrangement of the cells just after the third division. The division seems to be nearly simultaneous in all four cells and the wheel-formed group of eight results. This characteristic growth and elongation of the cells at this stage leads naturally to the oft-noted fact that the plane of the third division cuts that of the second obliquely rather than at right angles. A determining factor is, however, obviously the tendency to bisect the elongated cell at right angles to its major axis as well as the direct relation between the second and third cleavage planes. The elongation of the cells during division reminds one at once of the familiar elongation of the egg cell and other free globular cells at the time when the bipolar karyokinetic spindle figure is at its climax of development. We have no good figures of karyokinetic division in *Volvox* but Overton's figure from a 200-celled colony ('89, Taf. III, 18) shows telophase stages with the cells all elongated and the spindles in every case in the long axes of the cells.

It seems obvious that such a cell form in division implies a spindle figure with polar asters and justifies the assumption that the same internal forces are operating in the elongation of the *Volvox* cell as in the dividing egg. Typical polar asters may be expected to be found at such a stage as that shown in Overton's figure, like those shown by Swingle ('97) for a corresponding stage of division in *Sphacelaria*. We may conclude then that the adhesion of the four mother cells makes it necessary that the movement of material preparatory to the production of two equivalent rounded daughter cells should take place upon their free surfaces and the result is the characteristic bulging and elongation of the four cells during division. That this change of form is associated with the production of the karyokinetic figure with two polar asters seems clear from the figures of division in other alga cells with centrosomes. In any one of the cells of the four-celled group (Fig. 3, Pl. II), for example, if the third spindle figure has its axis 90° from that of the second division and in the same plane it is obvious that one of the asters will not have space for its full expression and if the adhesion of the quadrants is strong the yielding will be on

the free surface of the cell and tend to give us the oblong cell form shown in the figures. That elongation precedes or accompanies division is indicated by the number of oblong cells in the older colony shown in figure 7, plate II.

If the four cells should remain together and flattened upon each other the successive divisions at right angles would give very variously shaped and far from rounded daughter cells, as shown in Bütschli's diagram ('83, Fig. 1).

In effect, as viewed from the pole, the eight cells come to lie in an up-and-down zigzag line instead of forming an in-and-out zigzag, thus enabling each cell to remain as nearly as possible isodiametric without reducing the compactness of the group.

It has been generally agreed that each of the eight cells of the wheel figure divide to give a sixteen-celled stage and that the spherical or ellipsoidal form of the colony may be achieved (as it obviously is in sixteen-celled colonies of *Eudorina*) in this sixteen-celled stage.

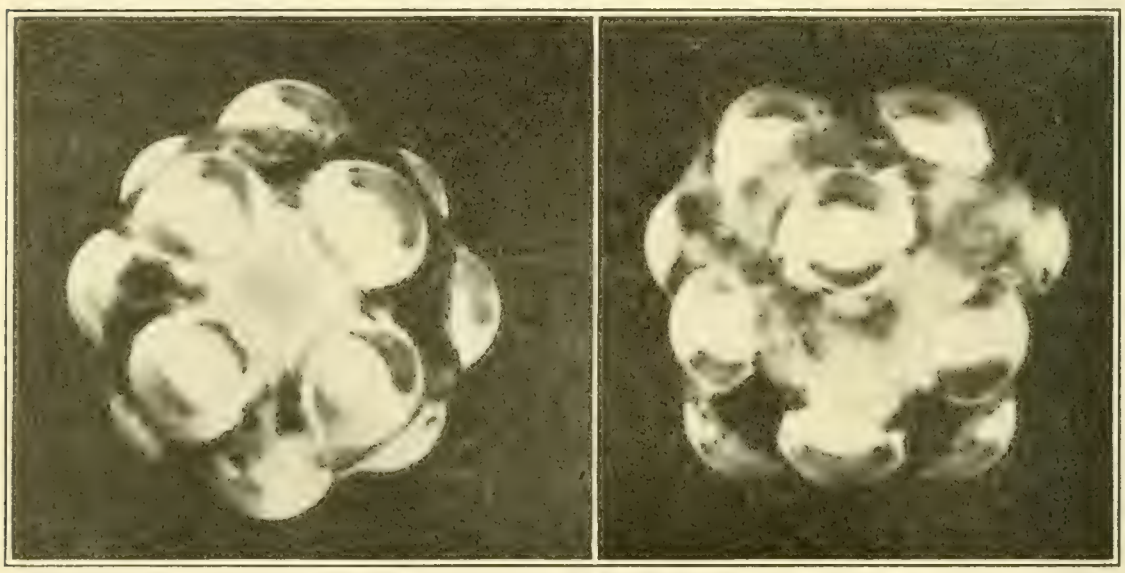
Goroschankin ('75) held that the 16- and even the 32-celled stage in *Eudorina* is a plate-shaped disk and that the transformation to a globular form came rather suddenly with the gelatinizing of the cell walls. He has not been followed in this view by later writers, though they have very generally been inclined to accept his account of the order of the cell divisions. Braun ('75), Bütschli ('83), Overton ('89), Klein ('90), and others hold that the spherical or rounded form of the colony is practically achieved by the sixteen-celled stage.

The fourth division is then a binary fission of all eight of the cells giving the sixteen-celled stage. The radial elongation of the four central cells on their free surfaces is followed naturally according to Hertwig's law by their transverse division. (See Klein's figure of *Eudorina*, '90, Taf. V, Fig. 63.) The four peripheral cells of the eight-cell stage also elongate before dividing, just as in the four-cell stage and divide transversely, giving the sixteen-celled group.

In *Gonium* the cells glide upon each other so as to form a series of groups of three with the central square opening, as I have pointed out elsewhere ('12). The greater adhesion of the four central cells in *Volvox* and the elongation of the cells before division prevent the *Gonium* configuration. The same situation develops as in the preceding third bipartition. There are eight new cells formed and these tend to more than fill the space on the margin of the curved disk of eight. Such a group is in very unstable equilibrium. The rounded shape of the mother-cell cavity influences the direction in which the cells glide upon each other, and adhesion tends to develop the compact groups of three. Of the eight new marginal daughter cells the four coming from the original group of four form a part of the equa-

torial series, while the four coming from the peripheral four cells of the eight-celled stage (Text-fig. 2) form a new polar group of four whose cells alternate with those of the original polar group. Henfrey ('56) described the sixteen-celled colony of *Eudorina* as consisting of two polar groups of four and an equatorial circle of eight cells.

Bütschli ('83) describes the sixteen-celled colony as consisting of four upper central cells, a ring of eight equatorial cells and four *lower* cells which alternate with the upper and gives a figure (Taf. XLV, Fig. 1, *i*). Overton's ('89) description of the arrangement of the cells in the eight-celled stage is essentially like that of Bütschli, though as Meyer notes, he ascribes the origin of the central cavity of the colony to the divergence of the cells in the four-celled stage and the subsequent hollowing out of the cells toward the center of the



1 2

FIGS. 1 AND 2. For explanation see text.

colony. Neither of these authors gives any very clear account of the arrangement of the eight equatorial cells or their relationship to the polar groups.

It is not easy to obtain satisfactory photographs of these sixteen-celled stages since, as noted, they are practically spherical and the number of cells is so small that no characteristic groups can be obtained in one focus. From a study of a large number of cases and photographs of various views I have been able to obtain data for the model made of marbles held together with wax and shown in two views in text-figures 1 and 2. Text-figure 1 shows the anterior pole of the young colony with the four cells forming a square, as has been observed by all students of the group. The opposite posterior pole of the colony would show a similar group of four, each cell alternating with the four at the posterior pole.

These are the relations of the two groups of four, as described by Bütschli and Overton. As noted, it is with reference to the position of the eight equatorial cells that clear description has been lacking. Text-figure 2 shows an equatorial view of the model and it is obvious at once that a least surface configuration requires the eight equatorial cells to form a zigzag belt, each cell alternating with two cells of the polar groups of four. With this arrangement the colony is made up of eight groups of three cells, the most compact arrangement possible, each of the four cells of each polar group appearing in two of the groups of three. The groups of three are so placed with reference to each other as also to form the groups of four seen in both the polar and equatorial views. The whole colony would consist of eight of these groups of four, since each of the eight equatorial cells is a member of three such groups and each cell of the polar group is a member of two such groups.

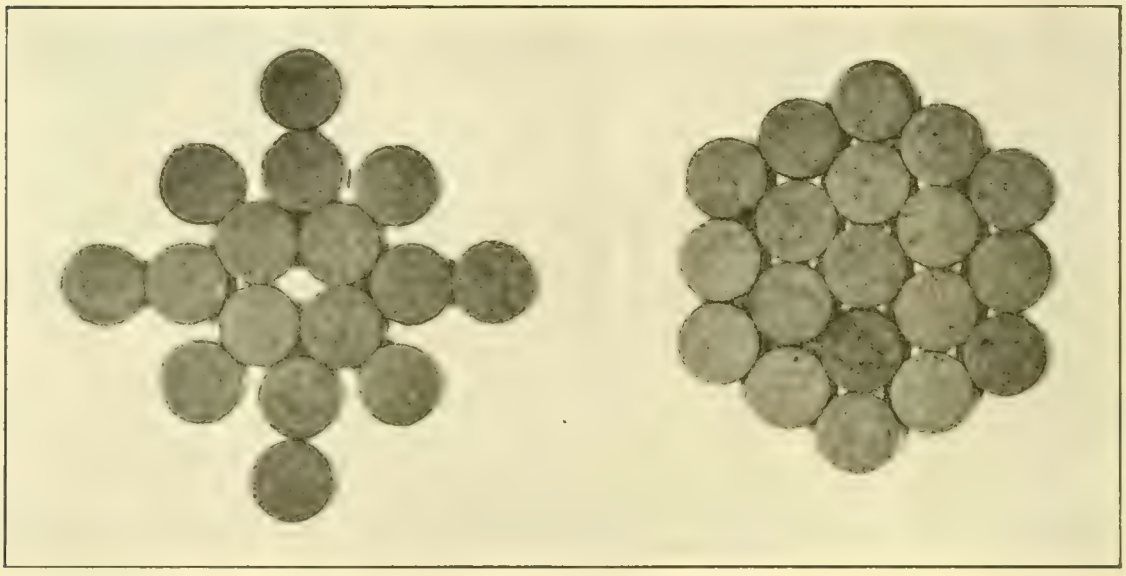
The whole forms as perfect an approximation to a least surface configuration as can be achieved by sixteen cells arranged in as nearly as possible a spherical group. Such a configuration may be regarded, it seems to me, as the type configuration and illustrates the interaction of surface tension, adhesion and binary fission as morphogenetic factors. In the actual colonies the cells are, of course, flattened upon each other and, as I have pointed out, elongate during division. As the photograph (Fig. 7, Pl. II) shows, they are quite variable in both form and size. As is shown clearly by Klein also in all figures of the so-called polar openings, phialopores, the posterior group of four do not form any such definite square group as is maintained by the anterior group of four, yet the tendency to the formation of the groups shown in the model is, it seems to me, obvious. The abundance of pentagons and hexagons in the cell outlines of the adult colonies is good evidence of a tendency to the most compact configuration possible.

I have not attempted to make the model with any great accuracy. We lack data as to the relative efficiency of adhesion and surface tension in the cells, which would be necessary for the exact determination of their interrelations. The actual relations of fission, adhesion and surface tension in the processes just described are perhaps brought out more clearly in the two diagrams (Text-figs. 3 and 4).

If the protoplasm of the mother cell were a mass which grows merely by imbibition and swelling, and if the cutting up of the mass into cells were merely a secondary phenomenon following the principle of the rectangular intersection of the cleavage planes and surface tension, as Hofmeister ('67), Sachs ('78), and other critics of the cell theory have assumed, we should expect a configuration of the cells like that shown in text-figure 4. This is the sort of configuration Magnus

('13) has obtained in his very interesting and suggestive experiment with paraffine wax cooling over mercury, a configuration determined entirely by the molecular forces operating in the system. It would be possible to form a sphere out of these nineteen units, but there is nothing in their number to favor the change from the discoid to the spherical grouping. To make a hollow or solid sphere out of such a group would involve very fundamental rearrangements.

On the other hand, if we make a diagram of the arrangement of the sixteen cells produced by binary fission, assuming for the sake of simplicity that each pair of daughter cells instead of remaining flattened upon each other with the resulting lateral displacement (Klein, Taf. VI, Figs. 61–63) rounds up completely after the third division and that the four cells first formed remain fixed by adhesion, we get the



3 4

FIGS. 3 and 4. For explanation see text.

configuration shown in text-figure 3. Here it is obvious that as contrasted with the arrangement in text-figure 4 it is a simple matter for the group to become cup-shaped and spherical simply by folding in the radial series and that the four outermost cells will come together in a group of four with its members alternating with those of the original group of four.

The group produced by binary fission in two planes with elongation of the cells upon their free surfaces and strong adhesion tends naturally, especially in the cavity of a spherical mother cell, to produce a globular young colony at the sixteen-celled stage.

As noted, all authors agree in maintaining that all the cells of the colony divide up to the sixteen-cell stage when the spherical form is practically complete. The later stages have not been followed.

Bütschli regards it as an open question whether all the cells divide in the later stages. It is, however, obvious that successive bipartition of all the cells is the natural method of maintaining the globular form already achieved. Any excess or deficiency of the number of divisions in any considerable group of cells would manifest itself at once as a bulge or depression in the surface of the expanding sphere unless compensatory divisions elsewhere and far-reaching, gliding movements of the cells among one another were possible. There is no evidence either of the occurrence or the possibility of such movements. As has been many times observed, the daughters of the original group of four can be recognized late in the life of the colony in their original positions with respect to each other and the colony as a whole.

Oltmanns ('04) follows Goebel ('82) and Goroschankin ('75) in asserting that this original polar group of four cells does not divide after the sixteen-cell stage but does not give any very positive evidence on the point. Overton ('89, Taf. III, Fig. 18) in a colony of about 200 cells shows a group of eight cells, six of which are dividing. It is, of course, obvious that a failure of the original group of four to continue dividing after the sixteen-celled stage would not prevent the maintenance of the rounded form of the colony in case there were compensating divisions in the adjacent cells.

It is interesting to note that Kirchner ('79) finds the development of the colony from the fertilized egg of *V. aureus* essentially like that of the asexual germ cell. His figures give some indication of the elongation of the cells before division and he describes the cup-shaped form of the colony in the eight-cell stage.

It seems to me that we are justified in concluding that *Volvox*, though showing deep-seated specialization of somatic and germ cells in which it contrasts markedly with *Eudorina*, *Pandorina* and *Gonium*, still like them shows vegetative totipotency and equivalence of its cells in the growth of the colony. This is an important consideration in view of the question as to the origin of the differentiation of germ and somatic cells which is so conspicuous in the adult colony of *Volvox*, and entirely lacking in the simpler members of the series. This differentiation is such that the germ cells are distributed solely in a single half or three fourths of the colony, the remaining portions remaining persistently somatic-sterile. The fertile area of the colony is regularly the posterior half or three fourths as the colony swims. It would be of great theoretical interest in this earliest appearance of the differentiation of soma and germ plasm if it could be shown that the cells bearing the germ plasm were different in cell lineage, age since last division, relative maturity as indicated by total number of divisions undergone, or in any other way, from the remaining cells of

the colony which show no capacity for reproduction and apparently undergo senile degeneration. If, for example, as is so commonly and loosely stated in textbooks, the colony were formed by marginal growth and cell division, forming first a curved plate and finally a sphere, so that the cells at one pole would be ontogenetically younger than those at the other, we might expect this to be the basis for differentiation of germ plasm and soma. The evidence is, however, that all the cells of the adult colony are of the same generation and ontogenetically equivalent.

The difference in their behavior is to be sought, then, in their relative environment and internal development as the colony grows. Their position in the posterior portion as the colony swims and around the pole which is nearest the point of connection between daughter colony and mother colony are obvious epigenetic factors in their environment which may be of significance. The distribution of the parthenogonidia at relatively equal intervals may be due to diffusion phenomena affecting nutrition directly or as stimuli, the whole complex perhaps suggesting analogy with Liesegang phenomena.

The attempt to differentiate the eight daughter colonies commonly formed in asexual colonies of *V. globator* as descendants of the eight cells produced by the third division seems to me wholly artificial. This third division is not essentially different from the other divisions. In *V. aureus* also the number of daughter colonies varies.

Meyer ('95) notes that the protoplasmic connecting strands between the cells are more numerous in this region of the germ cells than in the anterior part of the colony. They are especially well developed between the germ cells and the sterile cells as Janet's diagrams show so strikingly ('12, Fig. 4). It is also in this region, as noted, that the young colony maintains its connection with the mother colony through protoplasmic strands from the cells around the posterior polar opening which connect with the adjacent cells of the parent as shown by Overton ('89, Taf. III, Fig. 16), and Janet ('12, Fig. 1). The germ cells are borne then in that region of the colony which up to birth was most directly connected with the mother colony and perhaps received from it a large amount of food materials in the early growth stages.

The antheridia of *V. globator* form the so-called packets of antherozoids consisting of bundles of sixteen to thirty-two gametes. These are formed by binary fission of the mother cell in two planes. The eight-cell stage shows the wheel figure. The cells instead of forming a globular colony ordinarily form a flat plate like the simpler *Gonium*. Whether this is really due to a tendency to recapitulation retained in the sexual germ-cell formation or whether it is due to the elongation

of the male gametes as they form, is not clear, though it is generally agreed that the cell arrangement in the bundle of male gametes is homologous with that of the young vegetative colony.

Klein ('97) describes colonies of antherozoids in the form of hollow spheres. Stein ('78) had also observed them. Chodat ('02) reports plate-shaped individuals of *Pandorina*. These cases indicate how closely the plate-shaped and the spherical colonies are related physically. The globular antherozoid bundles in *Volvox* may well be regarded as tending toward the vegetative and away from the sexual condition. That such changes should involve changes in surface tension and adhesion is quite conceivable, as the elongation of the antherozoid cell body must of course be a factor in determining the form of colony. The further study of the formation of these abnormal male colonies, especially, should throw light on the whole series of morphogenetic problems here involved. The facts as known are certainly quite in harmony with the view that such presumably easily influenced factors as adhesion and surface tension, combined with the more fundamental and ever-present incompatibility between the principles of binary fission and least surfaces, may be of determining significance in the transition from the plate-shaped to the three-dimensional globular form of colony with all its evolutionary significance.

## INDEX OF LITERATURE

**Cohn, F.** Untersuchungen ueber die Entwickelungsgeschichte der mikroskop. Algen u. Pilze. Nova acta Leop.-Carol. 24 (1): 101. 1854.

**Henfrey, A.** Notes on Some Fresh-water Confervoid Algae. Trans. Mic. Soc. London, N. S., IV, p. 49. 1856.

**Hofmeister.** Die Lehre von der Pflanzenzelle. Leipzig. 1867.

**Braun, Al.** Bemerkungen zu Cohn's Schrift ueber Volvox. Sitz.-Ber. d. Ges. naturf. Freunde zu Berlin, Bot. Z. 190. 1875.

**Braun, Al.** Ueber einige Volvocineen. Sitz.-Ber. d. Ges. naturf. Freunde, Bot. Z. 189. 1875.

**Cohn, F.** Die Entwickelungsgeschichte der Gattung Volvox. Beitr. z. Biologie der Pflanzen 3: 93. 1875.

**Goroschankin.** Die Genesis bei den Palmellaceen. Versuch einer vergl. Morphologie der Volvocineae. Nachr. d. Kais. Ges. f. Naturw. usw. Moskau, 16. 1875.

**Sachs, J.** Ueber die anordnung der Zellen im jüngsten Pflanzenteilen. 1878.

**Stein, Fr. v.** Organismus der Infusionstiere. 3: 1. 1878.

**Kirchner.** Ueber die Entwickelungsgeschichte von Volvox minor. Cohn's Beitrage 3: 95. 1879.

**Goebel, K.** Grundzüge der Systematik und speziellen Pflanzenmorphologie. 1882.

**Falkenberg.** Die Algen. Schenk's Handbuch, p. 284. 1882.

**Bütschli.** Protozoa. Bronn's Klassen u. Ordn. d. Tierreichs. 1. 1883.

**Klebs, G.** Organization einiger Flagellatengruppen und ihre Beziehungen zu Algen und Infusorien. Arb. d. bot. Inst. Tübingen 1: 339. 1883.

**Klein, L.** Morphologische und biologische Studien ueber die Gattung Volvox. Pringsh. Jahrb. **20**: 133. 1889.

**Klein, L.** Neue Beiträge zur Kenntnis der Gattung Volvox. Ber. d. d. bot. Ges. **7**: 42. 1889.

**Overton, E.** Beitrag zur Kenntnis der Gattung Volvox. Bot. Centralbl. **39**: 65. 1889.

**Klein, L.** Vergl. Untersuchungen ueber Morphologie und Biologie der Fortpflanzung bei der Gattung Volvox. Ber. d. naturf. Ges. zu Freiburg i. B. **5**: 1890.

**Meyer, Arthur.** Ueber den Bau von Volvox aureus Ehrb. und V. globator Ehrb. Bot. Centralbl. **63**: 225. 1895.

**Swingle, W. T.** Zur Kenntnis der Kern- u. Zellteilung bei den Sphacilariaceen. Prings. Jahrb. **30**: 299. 1895.

**Kofoid, L. A.** Plankton Studies. II. On Pleodorina illinoisensis, a New Species from the Plankton of the Illinois River. Bull. Ill. State Lab. Nat. Hist. **5**: 273. 1898.

**R. Chodat.** Algues vertes de la Suisse. Berne. 1902.

**Oltmanns.** Morphologie u. Biologie der Algen, Jena, 1904.

**Harper, R. A.** The Structure and Development of the Colony in Gonium. Trans. Am. Mic. Soc. **31**: 65. 1912.

**Janet, C.** Le Volvox. Limoges, 1912.

**Magnus, W.** Ueber zellenförmige Selbst-differenzierungen aus flussiger Materie. Ber. d. d. bot. Ges. **31**: 290. 1913.

**Harper, R. A.** On the nature of types in Pediastrum. Mem. N. Y. Bot. Gard. **6**: 91. 1916.

## DESCRIPTION OF PLATE II

All figures of asexual reproduction in *Volvox* taken with Zeiss apochrom, objectives and the compensating eye-pieces.

FIG. 1. Two-celled stage of young colony. × about 600.

FIG. 2. Second division just completed. × about 600.

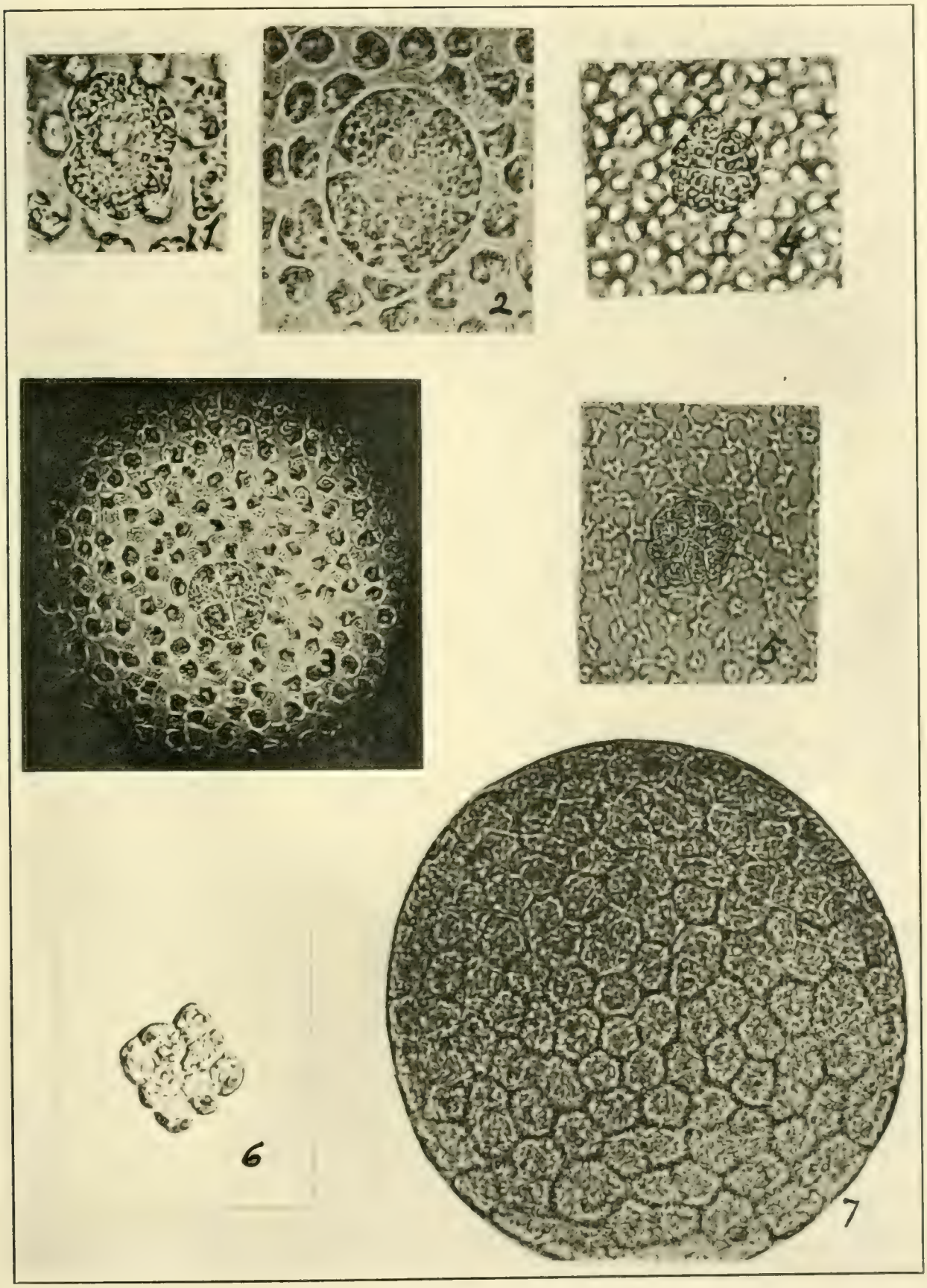
FIG. 3. Four-celled stage of young colony. × about 350.

FIG. 4. Four-cell stage, one cell elongating preparatory to third division. × about 350.

FIG. 5. Eight-cell stage showing the wheel or radial arrangement of the cells. × about 350.

FIG. 6. Same stage as last. The young colony photographed after being teased out of the mother cell. × about 400.

FIG. 7. Young colony not yet set free from mother colony and cell walls not yet gelatinized. × about 400.




HARPER: BINARY FISSION IN VOLVOX

# FURTHER STUDIES ON THE INTERRELATIONSHIP OF MORPHOLOGICAL AND PHYSIOLOGICAL CHARACTERS IN SEEDLINGS OF PHASEOLUS[1]

J. ARTHUR HARRIS

*Station for Experimental Evolution, Cold Spring Harbor, N. Y.*

## Introductory Remarks

In a series of papers published during the past several years I have emphasized the importance of investigations of the relationship between the morphological and the physiological characteristics of the organ and of the organism.

The structural variations of the organs of which the organism is made up are the resultant of intrinsic and extrinsic factors—of heredity and environment, or of nature and nurture. Morphogenetic processes must, therefore, be investigated by physiological methods, and be interpreted in physiological, and ultimately in physical and chemical, terms.

The purpose of this paper is to supplement and extend the results of an earlier study[2] in which it was shown that in bean seedlings characterized by certain morphological variations from type, the development of primordial leaf tissue is less than in normal controls grown under conditions as nearly as possible identical. The data then available indicated that a reduction of the volume of primordial leaf tissue is associated with abnormalities of all the types studied, but that the type of variation influences, in some degree, the amount of reduction.

In these first experiments the conclusions were based on primordial leaves only.

The use of such leaves has the obvious disadvantage that they are completely formed in the seed, and undergo merely an enormous expansion (and an undetermined amount of differentiation) in the

[1] Studies on the Correlation between Morphological and Physiological Characters, V. Studies I–IV of the series are to be found in Genetics 1: 185–196. 1916; 2: 186–212. 1917; 2: 282–290. 1917.

[2] Harris, J. Arthur. Studies on the Correlation of Morphological and Physiological Characters: The Development of the Primordial Leaves in Teratological Bean Seedlings. *Genetics* 1: 185–196. 1916.

germination of the seed and the development of the plantlet to the stage at which measurements were made.

Since the development of the primordial leaves during the germination and establishment of the seedling is relatively great, it seemed quite legitimate to use the weight of green tissue produced by these leaves as a measure of the physiological capacity of seedlings of various types. The fact that these leaves are differentiated in the seed, does, however, constitute a valid objection against their use as a measure of the physiological capacity of the seedling. For such purposes a constant based upon some organ developed later in the life of the individual is desirable.

One of the purposes of this paper is to present the results of determinations upon a later developed organ. The one chosen is the first trifoliate leaf.

This leaf was used because groups of plants of a higher degree of uniformity can be selected at the time of maturity of this leaf than at any later stage in the development of the plant, and because the first compound leaf reaches a degree of maturity sufficient for the purposes of the present study before the primordial leaves are too old to be used for a series of determinations. It is, therefore, possible to repeat, at a slightly later stage of development of the plant, the determinations made on the primordial leaves in the first study as a basis of comparison with the work already done and with the series of constants to be obtained for the first compound leaves of the same plants.

In the first investigation the green weight of the leaf tissue served as the fundamental measurement. In addition to this character certain measurements on the sap properties were also made. In the study of the saps some difficulties were encountered, and it seemed most desirable to discontinue that phase of the study temporarily and to carry out determination of dry weight and water content instead. These new measurements have, therefore, been added to these for green weight.

## Materials and Methods

The materials upon which this study is based are the same as those previously employed—a mixture of slightly different strains of navy beans. The seeds which were germinated in the fall and winter months of 1916 were grown in field cultures in 1915.

Seeds from individual plants were germinated in sand. In sorting, the morphologically aberrant seedlings were laid aside with a normal plant to serve as a check for each abnormal. An abnormal and a control seedling *from the same seed plant and germinated in the same*

*seed flat* were potted side by side in a three inch pot and allowed to grow to the proper stage of maturity under conditions as favorable as we were able to give them.

Before the samples were taken, the plants were carefully inspected and all pairs, one member of which had died, had been injured or which showed in its subsequent development any abnormality in addition to these specified were discarded. Note that there was no *direct* selection for the characters of the abnormal plantlets in this process, since both abnormal and control were discarded if *either* was unsuited for the purposes of the experiment.

There probably was a fairly stringent *indirect* selection, since the death rate and the mutilation rate of the variant individuals was probably greater than that of the normals. Thus more pairs were probably discarded because of an injury to or the death of the abnormal member of the pair than because of the death or injury of a normal member.

The probability that the materials were somewhat selected before the physiological measurements discussed in this paper were carried out renders the findings of greater significance than they would otherwise be.

After the pairs of seedlings had grown until the first compound leaf had attained its full size, and the second compound leaf was developing, but before the primordial leaves had materially deteriorated, samples of leaves were taken by nipping off the laminae only, or the laminae and the single petiolule of the terminal leaflet in the case of the compound leaf. These samples of tissues, each from 100 plants, were enclosed in flasks, weighed, and dried to constant weight in a bath surrounded by boiling water.

Thus the technique employed was exceedingly simple. Because of the size of the samples dealt with, the relative infrequency of the abnormalities, and the large number which had to be discarded, the routine has been excessively laborious. For example, the weighings of the 23 samples and checks discussed in the present paper involve 13,800 leaves gathered from 4,600 plants which were secured by germinating and classifying nearly half a million seedlings.

The structural variation in the bean seedling which is probably the simplest, and the most frequent, is a slight vertical separation of the cotyledons which are normally sensibly opposite in insertion. The amount of the separation is difficult to express quantitatively, since it is in some degree dependent upon the length of the axis. In our studies of seedling variation in Phaseolus, three grades of separation of the cotyledons have been recognized. The line of demarcation between these grades is a quite arbitrary one. This is also true of

the line between "normal," and "abnormal" as applied to the distinction between plants which have cotyledons inserted on the same level and those which have one of the pair sensibly higher on the axis than the other. "Slightly but distinctly separated," has been the descriptive term used in our classification schedules. The cotyledons range in position from those which are just perceptibly not inserted on the same level to those which are perhaps two or three or four millimeters apart. So imperceptible is the line of distinction between normal and abnormal plants that in the classification of the seedlings frequent discussions arose concerning the normality or abnormality of individual plants.

In the present paper I am considering only the simplest type of abnormality. This course has been followed for two reasons.

First, the proof of the existence of a physiological differentiation associated with a very slight structural variation is of far greater interest than the demonstration of measurable physiological differentiation associated with great morphological variation. Second, other types of abnormality with which I have dealt are so difficult to secure in satisfactorily large series that the number of samples as yet available is not sufficient to justify detailed comparisons between the different types of abnormality. I hope ultimately to be able to meet these difficulties. For the present the one type of structural deviation dealt with serves to illustrate the method and one phase of the results of the investigations.

## Presentation of Data

Consider first of all the green weight of the organs selected.

The average green weight of the primordial and of the first compound leaves for plants which are normal except for slight separation of their cotyledons is shown in Table I.

With one single exception, the average weight of the primordial leaves of the normal plants is higher than that of the abnormal plants. In the single exception to the rule, the difference is small in amount. The average weight of the first compound leaf produced by abnormal plants of this class is in every case but one lower than the weight produced by the sensibly normal individuals. The exception to the rule is the same sample as in the case of the primordial leaves.

The average weight of primordial leaf tissue in the abnormal plants is .5873, the average weight for normal plants is .6680, and the average difference −.0807. The differences in mean weights range in the individual samples from +.0074 to −.1286. For the first compound leaf of the same plants the average weight of the tissues from abnormal individuals is .4797, from a normal plant it is .5610, while the average

difference between the sample and the control is −.0813. The differences in average weight vary from +.0368 to −.2492.

TABLE I

*Mean Green Weight per Plant of Primordial Leaves and of First Compound Leaf*

| Sample | Primordial Leaves | | | | First Compound Leaf | | | |
|---|---|---|---|---|---|---|---|---|
| | Abnormal | Control | Difference | Percentage Difference | Abnormal | Control | Difference | Percentage Difference |
| 32 | .6034 | .7096 | −.1062 | 15.0 | .5132 | .5929 | −.0797 | 13.4 |
| 35 | .5648 | .6767 | −.1119 | 16.5 | .5444 | .6188 | −.0744 | 12.0 |
| 36 | .5951 | .6361 | −.0410 | 6.4 | .5931 | .6254 | −.0323 | 5.2 |
| 39 | .5619 | .6277 | −.0658 | 10.5 | .5160 | .5549 | −.0389 | 7.0 |
| 40 | .6096 | .7052 | −.0956 | 13.6 | .5179 | .6138 | −.0959 | 15.6 |
| 41 | .6068 | .7304 | −.1236 | 16.9 | .4877 | .6140 | −.1263 | 20.6 |
| 42 | .5879 | .6141 | −.0262 | 4.3 | .4712 | .7204 | −.2492 | 34.6 |
| 43 | .6222 | .7508 | −.1286 | 17.1 | .5008 | .6115 | −.1107 | 18.1 |
| 46 | .5956 | .7160 | −.1204 | 16.8 | .4645 | .6019 | −.1374 | 22.8 |
| 47 | .7058 | .6984 | +.0074 | 1.1 | .5841 | .5473 | +.0368 | 6.7 |
| 48 | .6389 | .7272 | −.0883 | 12.1 | .5593 | .6395 | −.0802 | 12.5 |
| 49 | .5902 | .6674 | −.0772 | 11.6 | .4960 | .5851 | −.0891 | 15.2 |
| 53 | .5402 | .5990 | −.0588 | 9.8 | .4491 | .4948 | −.0457 | 9.2 |
| 54 | .5720 | .6530 | −.0810 | 12.4 | .4091 | .4547 | −.0456 | 10.0 |
| 56 | .5380 | .5921 | −.0541 | 9.1 | .3994 | .4646 | −.0652 | 14.0 |
| 61 | .5193 | .5827 | −.0634 | 10.9 | .4443 | .4811 | −.0368 | 7.6 |
| 64 | .5853 | .7052 | −.1199 | 17.0 | .4530 | .5848 | −.1318 | 22.5 |
| 65 | .5747 | .6938 | −.1191 | 17.2 | .4402 | .5717 | −.1315 | 23.0 |
| 66 | .5886 | .6790 | −.0904 | 13.3 | .5246 | .5960 | −.0714 | 12.0 |
| 70 | .6853 | .7066 | −.0213 | 3.0 | .4794 | .4998 | −.0204 | 4.1 |
| 71 | .5639 | .6059 | −.0420 | 6.9 | .4132 | .4534 | −.0402 | 8.9 |
| 72 | .5565 | .6744 | −.1179 | 17.5 | .3799 | .4882 | −.1083 | 22.2 |
| 73 | .5033 | .6140 | −.1107 | 18.0 | .3933 | .4887 | −.0954 | 19.5 |

If these differences be reduced to percentages by using the weight of the normal plants as a base, as shown in the final columns of each section of the tables, it appears that the primordial leaves of the morphologically aberrant plants are from 3.0 to 18.0 percent lighter than the leaves of the normal plants in the 22 samples in which this relationship between the two types of plants holds for the primordial leaves. Thus the percentages are highly variable. The average for the 23 determinations is 11.95 percent. In the case of the first compound leaves, the percentage reduction ranges from 4.1 to 34.6 with an average of 14.06 in the 23 samples. Note that the percentage shows that the difference between the abnormal and the control sample is far less in the case of the single exception, sample 47, than it is in the average series. Thus it is only 1.1 as compared with an average value of 11.95 for the primordial leaves and only 6.7 as compared with the average of 14.06 percent in the compound leaves.

I now turn to a consideration of dry weight.

The primordial leaves of the abnormal plants in which the two cotyledons are slightly separated are, as shown in Table II, lighter

TABLE II

*Mean Dry Weight per Plant of Primordial Leaves and of First Compound Leaf*

| Sample | Primordial Leaves | | | | First Compound Leaf | | | |
|---|---|---|---|---|---|---|---|---|
| | Abnormal | Control | Difference | Percentage Difference | Abnormal | Control | Difference | Percentage Difference |
| 32 | .0445 | .0537 | −.0092 | 17.1 | .0442 | .0517 | −.0075 | 14.5 |
| 35 | .0366 | .0483 | −.0117 | 24.2 | .0465 | .0530 | −.0065 | 12.3 |
| 36 | .0422 | .0457 | −.0035 | 7.7 | .0476 | .0499 | −.0023 | 4.6 |
| 39 | .0409 | .0467 | −.0058 | 12.4 | .0430 | .0470 | −.0040 | 8.5 |
| 40 | .0438 | .0511 | −.0073 | 14.3 | .0415 | .0496 | −.0081 | 16.3 |
| 41 | .0431 | .0526 | −.0095 | 18.1 | .0406 | .0494 | −.0088 | 17.8 |
| 42 | .0416 | .0504 | −.0088 | 17.5 | .0383 | .0519 | −.0136 | 26.2 |
| 43 | .0429 | .0532 | −.0103 | 19.4 | .0391 | .0493 | −.0102 | 20.7 |
| 46 | .0408 | .0501 | −.0093 | 18.6 | .0400 | .0492 | −.0092 | 18.7 |
| 47 | .0442 | .0446 | −.0004 | .9 | .0442 | .0433 | +.0009 | 2.1 |
| 48 | .0420 | .0464 | −.0044 | 9.5 | .0444 | .0525 | −.0081 | 15.4 |
| 49 | .0381 | .0436 | −.0055 | 12.6 | .0397 | .0472 | −.0075 | 15.9 |
| 53 | .0365 | .0410 | −.0045 | 11.0 | .0399 | .0427 | −.0028 | 6.6 |
| 54 | .0384 | .0445 | −.0061 | 13.7 | .0339 | .0412 | −.0073 | 17.7 |
| 56 | .0349 | .0491 | −.0142 | 28.9 | .0331 | .0395 | −.0064 | 16.2 |
| 61 | .0356 | .0402 | −.0046 | 11.4 | .0383 | .0417 | −.0034 | 8.2 |
| 64 | .0354 | .0438 | −.0084 | 19.2 | .0341 | .0435 | −.0094 | 21.6 |
| 65 | .0357 | .0410 | −.0053 | 12.9 | .0344 | .0398 | −.0054 | 13.6 |
| 66 | .0354 | .0395 | −.0041 | 10.4 | .0381 | .0439 | −.0058 | 13.2 |
| 70 | .0426 | .0465 | −.0039 | 8.4 | .0407 | .0438 | −.0031 | 7.1 |
| 71 | .0279 | .0303 | −.0024 | 7.9 | .0274 | .0299 | −.0025 | 8.4 |
| 72 | .0273 | .0407 | −.0134 | 32.9 | .0265 | .0392 | −.0127 | 3.2 |
| 73 | .0298 | .0378 | −.0080 | 21.2 | .0315 | .0408 | −.0093 | 22.8 |

than those of the normal controls in every instance. The average dry weight of the abnormal is .0382, that of the control .0452 and the average difference is −.0070 grams. If the differences be expressed as a percent of the control value as a base, they range from less than 1 to nearly 33 percent, with a general average of 15.21 percent.

The results for the first compound leaf are very similar. In 22 of the 23 cases the primordial leaves of normal plants yield a greater weight of dry substance than those of the abnormal plants. The exception to the rule is again sample 47. The average dry weight of the first compound leaf of abnormal plants is .0385, that of normal plants is .0452 and the average difference is −.0067 grams. If the differences be expressed as percentages of the control constants they are seen to range from 3.2 to 26.2, for the 22 series in which the abnormal plants produce a smaller amount of dry substance. The difference in the single exceptional series is small, only 2.1 percent as compared with a general average of 13.36 percent in the 23 samples.

Having shown that the abnormal plants produce both a smaller green weight and a smaller dry weight in both the primordial and in the first compound leaves, the problem of the relative quantities of water and dry materials in the leaves of the two types of plants naturally presents itself for consideration.

The results have been expressed in terms of the percentage of dry substance in the leaves, *i. e.* (dry weight × 100)/green weight. The constants appear in Table III.

TABLE III

*Percent of Dry Matter in Primordial Leaves and in First Compound Leaf*

| Sample | Primordial Leaves | | | First Compound Leaf | | |
|---|---|---|---|---|---|---|
| | Abnormal | Control | Difference | Abnormal | Control | Difference |
| 32 | 7.374 | 7.567 | − .193 | 8.612 | 8.703 | − .091 |
| 35 | 6.480 | 7.137 | − .657 | 8.541 | 8.564 | − .023 |
| 36 | 7.091 | 7.184 | − .093 | 8.025 | 7.978 | + .047 |
| 39 | 7.278 | 7.439 | − .161 | 8.333 | 8.469 | − .136 |
| 40 | 7.185 | 7.246 | − .061 | 8.013 | 8.080 | − .067 |
| 41 | 7.103 | 7.201 | − .098 | 8.324 | 8.045 | + .279 |
| 42 | 7.076 | 8.207 | −1.131 | 8.128 | 7.204 | + .924 |
| 43 | 6.894 | 7.085 | − .191 | 7.807 | 8.062 | − .255 |
| 46 | 6.850 | 6.997 | − .147 | 8.611 | 8.174 | + .437 |
| 47 | 6.262 | 6.386 | − .124 | 7.567 | 7.912 | − .345 |
| 48 | 6.574 | 6.381 | + .193 | 7.938 | 8.210 | − .272 |
| 49 | 6.455 | 6.533 | − .078 | 8.004 | 8.067 | − .063 |
| 53 | 6.757 | 6.845 | − .088 | 8.884 | 8.629 | + .255 |
| 54 | 6.713 | 6.815 | − .102 | 8.286 | 9.061 | − .775 |
| 56 | 6.487 | 8.293 | −1.806 | 8.287 | 8.502 | − .215 |
| 61 | 6.855 | 6.899 | − .044 | 8.620 | 8.668 | − .048 |
| 64 | 6.048 | 6.211 | − .163 | 7.528 | 7.438 | + .090 |
| 65 | 6.212 | 5.909 | + .303 | 7.815 | 6.962 | + .853 |
| 66 | 6.014 | 5.817 | + .197 | 7.263 | 7.366 | − .103 |
| 70 | 6.216 | 6.581 | − .365 | 8.490 | 8.764 | − .274 |
| 71 | 4.948 | 5.001 | − .053 | 6.631 | 6.595 | + .036 |
| 72 | 4.906 | 6.035 | −1.129 | 6.976 | 8.029 | −1.053 |
| 73 | 5.921 | 6.156 | − .235 | 8.009 | 8.349 | − .340 |

The results are not so consistent as those for the absolute values, green weight and dry weight. This condition is to be expected for two reasons. First, the abnormal plants show lower values of both green weight and dry weight than the normal controls. One cannot, therefore, expect such large differences in the indices calculated from these constants as if both measures did not differ in the same direction between abnormal and control series. Second, two sets of technical operations are involved in the indices, only one in each of the constants used in calculating these ratios. While every effort to avoid error was made, the probabilities of error in an index are clearly twice as great as in either of the constants upon which it is based.

Notwithstanding these two sources of difficulty in basing conclusions on relative amount of dry substance, there seem clear evidences that the abnormal plants produce relatively as well as absolutely less dry matter than the normals.

In the case of the primordial leaves, there are 20 samples in which the relative dry weight is lower in the abnormal plants as against 3 in which it is higher. In the first compound leaf there are 15 samples in which the relative weight in the abnormal plants is lower, as compared with 8 in which it is higher than the normals.

The average percentage content of dry substance in the primordial leaves of the abnormal seedlings is 6.509 as compared with 6.779 in the normal controls, or a difference of −0.270. The average percent of dry matter in the first compound leaf is 8.030 in the abnormal as compared with 8.080 in the normal, or a difference of −.050 percent.

## Concluding Remarks

The constants recorded in this paper are the results of one of the phases of an attempt to determine the nature of the relationship between morphological and physiological variations in plants.

The results of the criteria applied are beautifully clear and consistent.

Seedlings of *Phaseolus* which show one of the smallest definite structural variations, the slight vertical separation of the two cotyledons in their insertion on the axis, are differentiated from the structurally apparently normal individuals in their physiological as well as in their morphological characteristics.

This is shown by the facts that the morphologically abnormal plants produce a smaller weight of green leaf tissue, a smaller actual weight of dry substance in the leaf tissue, and a smaller relative weight of dry substance. This is true for both the primordial leaves and the first trifoliate leaf.

# AMERICAN HEATHS AND PINE HEATHS

JOHN W. HARSHBERGER

*University of Pennsylvania*

One of the attempts of modern phytogeography and ecology has been to establish an exact nomenclature and to correlate the existing knowledge of the fundamental units of vegetation the world over. The thought of the leading phytogeographers has been to limit the use of descriptive terms to an exact meaning, following the lead of the earlier morphologists, who, like Linnaeus, made an exact science of morphology out of a chaos, or jumble, of inexactly applied descriptive terms. The earlier morphologists had somewhat of an advantage, because they were applying names to parts of plants which had no recognition as such by the laity, and where in common usage, the concept of such words as bract, carpel, ovule, and the like, had no application. The phytogeographers, however, find that their concepts parallel those of the botanically uninitiated, who refer in everyday speech to forest, to meadows, to prairies, to marshes, to swamps and to heaths. Elsewhere[1] the writer has shown that country people have a keen appreciation of the fundamental differences in the native vegetation for they have applied names in a general and unscientific way to plant formations recognized by ecologists. Graebner[2] has emphasized this fact in his "Die Heide Norddeutschlands." If the phytogeographer adopts a local descriptive term he should attempt to strictly limit the use of the term to the same unit of vegetation. If this is done, then there can be no objection to the adoption of the descriptive name from the common speech of the people, who roughly distinguish a certain association of plants. Professor Diels on the other hand considers the use of vernacular names in plant geography very questionable. He maintains that such terms are ambiguous, even in the language to which they belong, that to persons of foreign birth they are either meaningless or liable to misunderstanding, that even if such terms are strictly defined, they will become confused again, and that they are permanently confusing to people unfamiliar

[1] Harshberger, John W. The Vegetation of South Florida. Wagner Free Inst. of Sci. Trans. 7[3]: 146. 1914. The Vegetation of the New Jersey Pine-barrens, p. 48. 1916.

[2] Graebner, Paul. Die Heide Norddeutschlands. Die Vegetation der Erde 5: 14. Leipzig. 1901.

with phytogeography. He believes that there should be universal expressions in Latin, or Greek, and to have these alone. I can heartily agree with the general opinion of Diels about the necessity of a stable nomenclature in plant geography, but it would be unwise to abolish vernacular terms, even if these are used with some confusion. As teachers in the class-room, in our published papers, in our conversation and in our encyclopedic work, if called upon to contribute articles to dictionaries and encyclopedias, we should try and clarify the ideas of the public on these essential points.

For example, the word forest is a *nomen confusum*. In its use, in England, a forest may signify any wild, open, uncultivated tract of land, not necessarily a tract of woodland, though historic documents prove that parts of the ancient forests of the British isles were covered with trees. The term forest in the United States fortunately is applied more exactly and properly to a tree-clad area. The same confusion is seen in the application of the words swamp, marsh and moorland. The natives of the island of Nantucket, and the visitors who have learned the name from the habitant, call typic heathland by the cognomen moor, and similarly in England, where the word heath is in common use, it is applied very inexactly. Heath to the Britisher is usually a heather-clad tract of land, yet in eastern England, the word is also used to denote a calcareous pasture with no heather, as Newmarket Heath and Royston Heath, and in Somerset, it is used to designate tracts of deep and often wet peat.

As the research investigations of the writer have led him to believe that certain types of vegetation in America correspond with the true heath and pine-heath of Europe, it becomes necessary to see if we can correlate the different usages of the word heath so as to unsnarl the tangle into which the use of the word seems to have fallen.

Tansley in the introduction to "Types of British Vegetation" (p. 2) states that heathland nearly always involves a relatively poor and dry soil. Under the climatic conditions of the British Isles, heath is found on shallow, dry, peaty soils dominated by the common ling (*Calluna vulgaris*) and occurs in regions of medium rainfall in the center, south and east, and on similar sandy soil in Belgium, Holland, Denmark and northwest Germany. The surface of the soil of such heaths is covered with dry peat (Trockentorf) with the general absence of deep peat. Where in hollows of true heathland with an impervious substratum, true moor peat is found, heath passes imperceptibly into moor, and hence there has often been confusion of the two kinds of phytogeographic concepts.

In "Types of British Vegetation" (pages 98–99) is given a statement as to the character of the heath formation of northwest Europe.

It is typically developed on relatively poor sandy and gravelly soils, whose climate is wetter than that which gives rise to steppe, the climate of which is too dry for tree growth. Heath may exist side by side with woods and may represent a degeneration of woodland. Heath occurs in Europe in regions with an annual rainfall between 25 and 40 inches (60 to 100 cm.), but the Cornish heath and those of the eastern Highlands of Scotland often receive a rainfall of between 40 and 60 inches (100 to 150 cm.) in the year. The Scottish heaths develop a deeper layer of relatively pure acid humus, up to 8 or 12 inches (20 to 30 cm.), according to Hardy. The East Anglian heaths have a rainfall of 25 inches, or less, and a minimum of dry peat formation, while the heaths of the southeastern counties have a layer of dry peat seldom more than a fraction of an inch in thickness passing down into sand darkened by humus. The surface layer of dry peat is formed by lichens and mosses, which are pioneers on denuded soils.

Drude in his comparison of the flora of Great Britain with that of Central Europe[3] believes that the lowland heaths, the "heath association" or "Callunetum arenosum" of Tansley, for the most part correspond with those of northwestern Germany in the region of the Weser and the Ems, and on the English heaths one would often feel oneself transported to Germany, if it were not for the sudden occurrence of *Erica cinerea* between *Erica tetralix* and *Calluna vulgaris*, or of *Ulex minor*, or *Ulex gallii* with masses of *Schoenus nigricans*, *Myrica gale*, *Narthecium* and *Hypericum elodes*, which indicate the west European conditions.

If there is a physiognomic similarity in the heathland of England and northwest Europe, then we must determine the essential character of the heath vegetation and the kinds of soils on which it is found, for by extension we can apply these characters as a test of heathland in other parts of the world.

Although the soils of the North German plain are the same in the east as in the west, according to the researches of Graebner and others, yet the vegetation of the two areas is quite distinct. In the west, in Hanover, Oldenburg and Schleswig-Holstein, are great stretches of heathland, whilst in the east these are entirely absent and are replaced by thin pine woods (pine-heath = Kiefern-heide) and a steppe-like flora. This difference is due in part to the different climate, for the main heathland is west of the Elbe, where the rainfall rarely falls below 24 to 28 inches per annum, whereas in the east the rainfall often does not exceed 20 inches per annum. In other words, heathland is developed with an oceanic climate, while pine-heath is found where the climate is continental. The seasonal changes of temperature of

[3] The International Phytogeographic Excursion in the British Isles (1911), p. 93.

an oceanic climate are slight. The relative humidity is higher. There is a larger amount of cloudiness and a heavier rainfall than is found over continental interiors. Marine climate is equable. With a continental climate the annual temperature ranges increase, as a whole, with increasing distance from the ocean. The regular diurnal ranges are also large. The winters are cold and the summers are hot. Cloudless skies are more frequent and the air is dustier and drier.

In Europe, where heath plants grow, there is a formation of fibrous and slightly earthy humous layers, the undecomposed elements of which are deposited in dense masses to form the so-called "*raw-humus*," which in some cases is deposited as a thin peat layer. The humic

FIG. 1. Nantucket heath with pearly everlasting (*Anaphalis margaritacea*) and bayberry (*Myrica carolinensis*). August 20, 1914.

acid, according to Ramann, acts on the unweathered silicate, decomposing it energetically, bringing into solution alkalis and alkaline earths, leaches the soil, *i. e.*, the soluble substances are carried down to greater depths. If raw humus lies on sandy soils, the sand of the upper layers appears bleached and becomes light gray in color, being in this condition called lead sand. Below this light-colored layer is found a yellowish to brownish soil due to the grains of sand being mixed with ferric-oxid or ferric hydrate. The precipitated organic substances cement the separate sand grains into compacted layers

below the lead sand and meadow ore, and a humus sandstone is formed. This is called Ortstein and forms an impervious layer. The roots of pine trees are unable to penetrate this layer and flatten out on it. The pine trees become stunted, their branches gnarled and the tree finally dies to be replaced by others which pass through the same cycle unless the tap-root manages to pass through a hole into the subsoil.

The phytogeographic investigations of the writer have shown that on the island of Nantucket we have true heaths, called moors by the

FIG. 2. Bear oak (*Quercus nana*) in heathland, Nantucket. September 7, 1914.

inhabitants. Typic heather plants grow on the sandy and gravelly glacial soils of the island and there is a formation of dry peat on the surface of the soil. The low, rolling hills are covered with plants in different groupings, so that in places the western prairies are suggested, while in other places the Roman Campagna, especially where the vegetation has been browsed by cattle. The plain-like character of the vegetation is suggested in those areas where the beard grass (*Andropogon scoparius*) covers the ground in exclusive growth, except where patches of heath plants are found such as the huckleberry (*Gaylussacia resinosa*) and the bearberry (*Arctostaphylos uva-ursi*) (Figs. 3 and 4) which forms mats, or carpets of large extent. Another common plant, which suggests the Scotch heather (*Calluna vulgaris*),

is a plant with bright yellow flowers (*Hudsonia ericoides*), while with it we find associated the grayish patches of the reindeer moss (*Cladonia rangiferina*), hair moss (*Polytrichum*), goat's rue (*Tephrosia virginiana*), extensive masses of trailing arbutus (*Epigaea repens*), and patches of *Anaphalis margaritacea* (Fig. 1). Clumps of the bayberry (*Myrica carolinensis*) of a dark green color break the monotonous level of the heath (Figs. 1 and 3). Patches of an irregular rounded form of the huckleberry (*Gaylussacia resinosa*) and sweet fern (*Comptonia asplenifolia*) are common. A few other flowering plants relieve the flat

Fig. 3. Granite boulder (crow-stone) surrounded with carpet of bearberry (*Arctostaphylos uva-ursi*), Nantucket heath. August 20, 1914.

green tones of the rolling surface, such as the wild indigo (*Baptisia tinctoria*), golden aster (*Chrysopsis falcata*) and white-topped aster (*Sericocarpus asteroides*).

Some parts of Nantucket, notably the southeastern, are covered by two low oaks, namely, the bear oak (*Quercus nana*) (Fig. 2), and the dwarf chestnut oak (*Quercus prinoides*). In some places on Nantucket and in central Marthas Vineyard, this growth of oaks and associated plants suggests the dwarf elfin wood, or chaparral, of the California coast. The other constituents of these low oak thickets are the bayberry (*Myrica carolinensis*), sweet fern (*Comptonia asplenifolia*) and the low spreading carpets of the bearberry (*Arctostaphylos*

*uva-ursi*) (Figs. 3 and 4). The growth of low oaks found over a large part of Nantucket and the central part of Marthas Vineyard may be looked upon as an oak-heath, because many of the associates of *Quercus nana* and *Q. prinoides* belong to the heath family. The soil conditions are such that a dry peat is formed over a subsoil of sand and gravel, just as we find in the heathland of European countries.

The island of Nantucket is also characterized by the presence of the broom-crowberry (*Corema Conradii*), which grows rather plentifully in the central part of the island (Fig. 5), and along Tom Never's Bluff. It forms on Nantucket round-headed clumps, which vary in

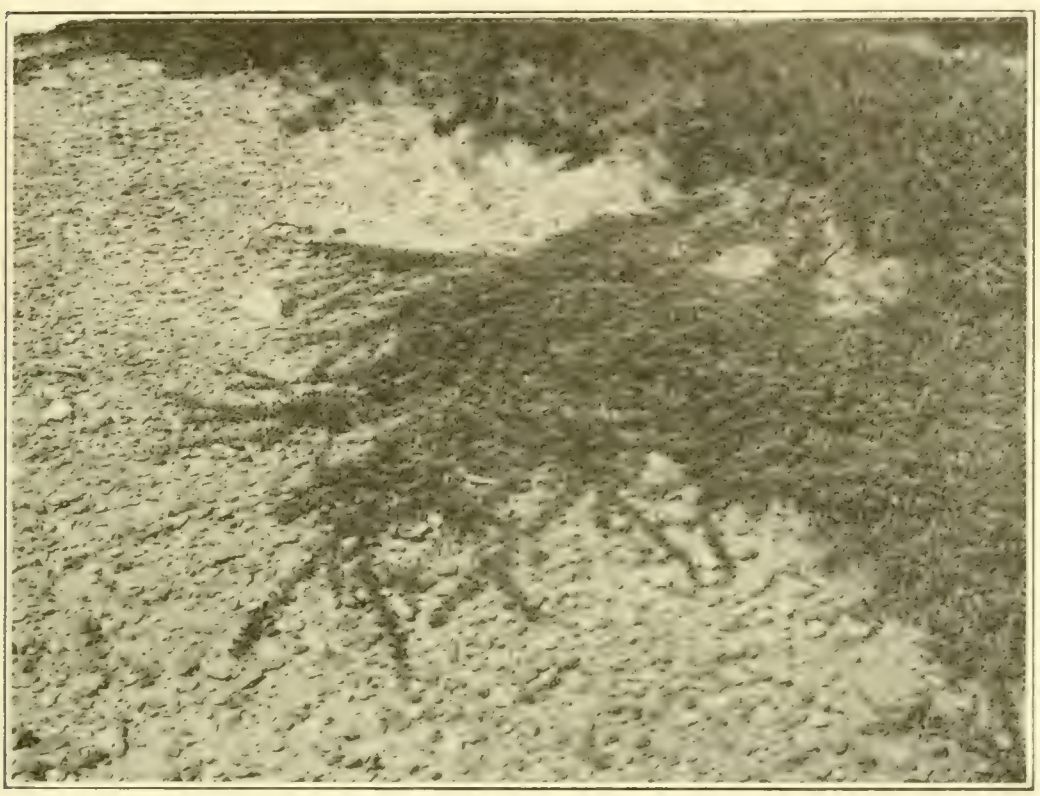


FIG. 4. Bearberry (*Arctostaphylos uva-ursi*) spreading over a denuded gravel slope, Nantucket. August 20, 1914.

size from a few feet across to many feet in diameter. Along Tom Never's Head, owing probably to the undermining of the bluff by the action of the surf, we find the plant mingling with the true beach plants of the upper sea beach. In New Jersey, the most local and peculiar plant of the Lower and Upper Plains is the broom-crowberry which grows in two general forms. The first type of plant is one which grows in dense cushions (Fig. 6) about 3 decimeters (1 foot) tall, its color varying from light green through dark green to a rich brown color, distributed in clumps between the prostrate pine trees. That this is the typic form is indicated by the fact that it is the type

found on Nantucket and elsewhere. The second type is the diffuse one, where the stems are scattered widely.

In New Jersey, *Corema Conradii* (Fig. 6) is associated with rounded, basket-like, dwarf pitch pines (*Pinus rigida*) along with bearberry (*Arctostaphylos uva-ursi*), huckleberry (*Gaylussacia resinosa*), sweet fern (*Comptonia asplenifolia*), trailing arbutus (*Epigaea repens*) and the like, so that this type of heath I have called a Coremal. Some facts may be learned about the vegetation of the New Jersey Coremal by contrasting it with the Coremal on the Island of Nantucket. The physiognomy is slightly different, owing to the absence of the dwarf

FIG. 5. Cushion of broom-crowberry (*Corema Conradii*), central part of Nantucket. September 5, 1914.

pines in the true Coremal of Nantucket. In both districts, there is a low vegetation of shrubby oaks, *Quercus nana* and *Q. prinoides*. The bearberry (*Arctostaphylos uva-ursi*) is more abundant on Nantucket (Figs. 3 and 4) than on the plains of New Jersey, while the broom-crowberry is found in both districts (Figs. 5 and 6). A comparison of the Nantucket vegetation gives a clue to the origin of the plains (Coremal) and the pine-barren vegetation of New Jersey. Heath-land is the result of the factors which are summed up under the general term oceanic climate, and Nantucket, isolated far out at sea, has an oceanic climate. The strong winds that blow and the pervious

glacial soils prevent the deciduous trees of large size from spreading out of the valleys, where they are protected, and even the pitch-pine, recently introduced into Nantucket, follows the valleys and protected slopes of the hills. In all probability, when the pine-barren region of New Jersey was an island, an oceanic climate prevailed. The typic heathland of which the Coremal is a part was left as a relict in the plains of New Jersey. The pine forest in those early times probably filled the valleys and later spread over the hills until all of the region was covered with pine forest except the areas represented by the Upper and Lower Plains, where edaphic conditions prevented the growth of tall pine trees. The heathland of this early time was

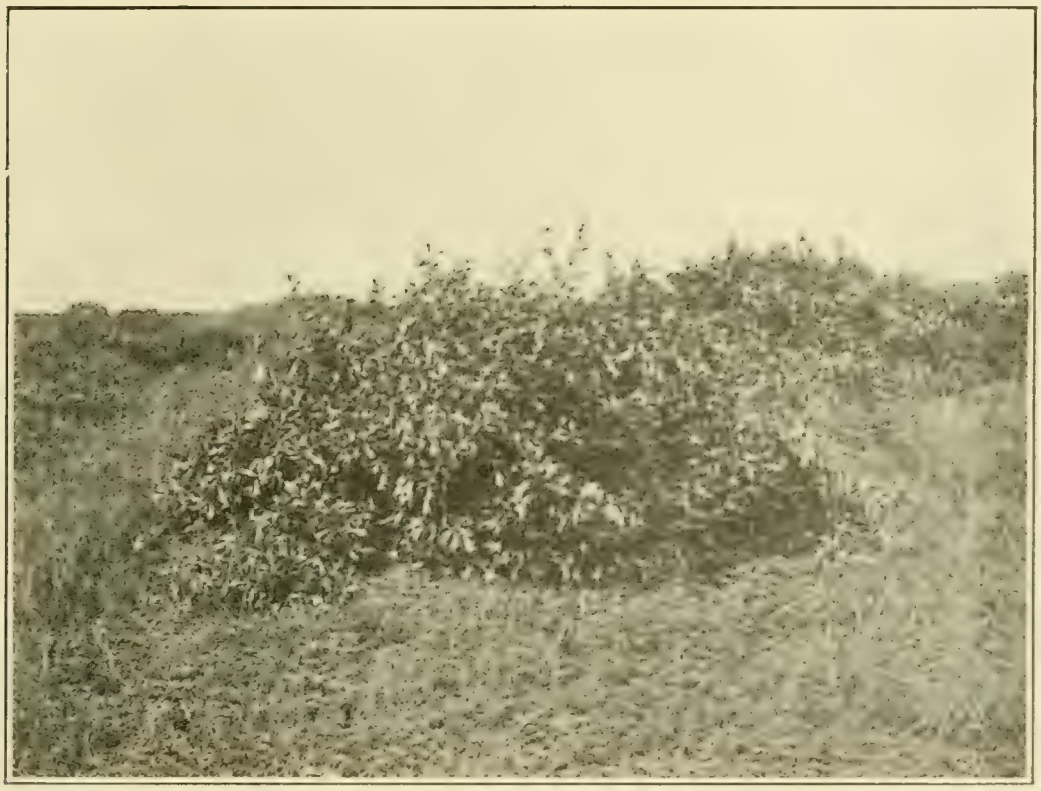


FIG. 6. Broom-crowberry (*Corema Conradii*) along cart road, Warren Grove, N. J. In flower, April 7, 1917.

finally converted into the present pine-heath. Graebner has detailed a similar conversion of heath into pine forest by the invasion of pines, and in such German pine forests the undergrowth consists of characteristic heath plants, hence the term Kiefern-heide applied to this pine forest with an undergrowth of heath plants.

The pine trees have been unable to grow to tall size in the New Jersey Coremal because of a hard layer of soil immediately below the upper sandy layer (Fig. 6). This layer corresponds to the caleche of Mexico, the plow-sole of agriculturists and the Ortstein of the Germans.

Klebahn[4] figures an Ortstein Kiefer where the tap-root striking the hardpan is bent over, being unable to penetrate that soil layer. Graebner narrates how such pine trees grow for a time, but finally, after reaching a certain age, begin to go back, or decline in vigor, until they succumb, and he describes how certain pine trees more fortunately situated by natural planting over holes through the Ortstein (Ortsteintöpfe) are able to send their tap-roots into the deeper soil layers.[5] Under such conditions tall thrifty pine trees will be scattered here and there over the surface of the heathland, while the majority of the trees, that become established in the region, are dwarf and

FIG. 7. Pine-barrens (pine-heath) near Lake Ronkonkoma, Long Island. July 20, 1913.

languishing. Similar conditions are found in the plains of New Jersey where the low, dwarf pine trees live for a number of years and finally succumb, to be replaced by other trees that pass through a similar existence. Hence the dwarf basket pines of the New Jersey Coremal are all short-lived. Thus hardpan and fire are the two most important factors which have perpetuated the heath vegetation of the New Jersey plains (Coremal), while the surrounding region with more

[4] Klebahn, H. Grundzüge der allgemeinen Phytopathologie, p. 14.

[5] Graebner, P. Die Heide Norddeutschlands. Die Vegetation der Erde 5: 125.

pervious soil, although similarly fire-swept in later years, has been preserved as a pine forest, or pine-heath (Kiefern-heide). Remove the pines and the conditions as they exist in the Coremal of Nantucket are duplicated. The New Jersey pine-barrens with the removal of the pines represent such an oak-heath as we have described for the islands of Marthas Vineyard and Nantucket and of similar physiognomy with such oaks as the bear oak (*Quercus nana*) and dwarf chestnut oak (*Quercus prinoides*) forming the main ground cover.

Similarly, as in Germany, the pine trees in the Long Island and New Jersey regions have become dominant and the heath plants in

FIG. 8. Rounded clumps of pine-barren heather (*Hudsonia ericoides*) in full flower growing one mile south of Shamong, N. J. May 27, 1916.

the form of the bearberry (*Arctostaphylos uva-ursi*), sand myrtle (*Dendrium buxifolium*), huckleberry (*Gaylussacia resinosa*), laurel (*Kalmia latifolia*), and the oaks become subordinate to the pines and form the characteristic undergrowth of the pine forest (Figs. 7 and 8). Graebner distinguished several types of heath woodland, as follows:

1. Type. Pine-heath.
   - Facies *a*. Pine-heath with dominance of *Juniperus communis*.
   - Facies *b*. Pine-heath with dominance of *Rubus* species.
   - *Facies *c*. Pine-heath with dominance of *Arctostaphylos uva-ursi*.

*Facies *d*. Pine-heath with dominance of grasses.
*Facies *e*. Pine-heath with dominance of *Vaccinium myrtillus* and *V. vitis-idaea*.
*Facies *f*. Pine-heath with bog-moss substratum.

2. Type. Broad-leaved Tree-heath.
Facies *a*. Birch-heath.
*Facies *b*. Oak-heath.

Those facies of the forest-heaths in Germany which are similar physiognomically with the ones in New Jersey are marked with an asterisk. Facies *e* in Germany, with the prevalence of two species of *Vaccinium*, is represented in New Jersey by a pine forest with an undergrowth of *Gaylussacia resinosa*, *Kalmia angustifolia*, *Vaccinium pennsylvanicum* and *V. vacillans*. The oak-heath we have described and also the heathland, where the bearberry is common, as on Nantucket.

We are able, therefore, by this comparative study to correlate certain American plant formations with those of Europe. The species of plants represented in each are in general different, but physiognomically the contrast can be made with general correctness.

| *America* | *Europe* |
|---|---|
| *Heathland* (with huckleberries, blueberries and bearberries, etc.). | *Heathland* (Heide, with heather, etc.). |
| *Oak-heath* (with low oaks, etc.). | *Oak-heath* (Eichen-heide). |
| *Coremal* (heathland with broom-crowberry in Nantucket with addition of dwarf pine on plains of New Jersey). | *Low pine-heath* (Kiefern-heide). |
| *Pine-barrens* (Long Island and New Jersey, incipient on Nantucket (Figs. 7 and 8)). | *Pine-heath* (Kiefern-heide). |

Much remains to be done in the study of the phytogeography of America, but we have reached a stage in our investigations where it is profitable to compare the American plant formations with those of Europe and other parts of the world. This comparison leads to a clarification of our concepts and also brings about a correlation of our knowledge, so that it is possible to formulate certain principles upon such comparative study. The three international phytogeographic excursions have done much to stimulate this kind of comparative investigation, where the studies of botanists in other climates and in other countries can be used for the extension of our knowledge of the fundamental principles upon which phytogeography, ecology and plant physiology depend.

# SOME BOTANICAL PROBLEMS THAT PALEOBOTANY HAS HELPED TO SOLVE

ARTHUR HOLLICK

*Museum of the Staten Island Association of Arts and Sciences*

Among the savants whose investigations in connection with the vegetable kingdom have earned for them the distinction of having their names graven on the walls of the laboratory building of the Brooklyn Botanic Garden are four to whom paleobotany lays claim, at least in part—Adolf Théodore Brongniart, Leo Lesquereux, Oswald Heer, and Marquis Gaston de Saporta—and it is my privilege briefly to outline some of the botanical problems which they and other paleobotanists have helped to solve.

Paleobotany, as a science, is much younger than botany. Living plants were noticed, studied and classified long before fossil plants had received any serious attention. In fact it was only a little more than a century ago that fossil plants began to be recognized as the probable actual remains of former living plants.

The science of paleobotany may be said to have been born in 1804, when Ernst Friedrich, Baron von Schlotheim, issued his Beschreibung Merkwürdiger Kraüter-Abdrücke und Pflanzen-Versteinerungen: ein Beitrag zur Flora der Vorwelt, generally known and cited as Schlotheim's Flora der Vorwelt, in which he discusses the prevailing theories in regard to the nature and origin of fossils, or "petrifactions" as they were commonly called at that time, and uses the following epoch-making words: ". . . and more recent observations and investigations have even led us to the very probable supposition that *they may be the remains of an earlier so-called pre-Adamic creation, the originals of which are now no longer to be found.* . . . In the continued investigation of this subject this opinion, with certain restrictions, has in fact gained a high degree of probability with the author of the present work, so that he ventures to announce his treatise as a contribution to the flora of the ancient world."

In the light of what we know and take for granted today this statement sounds strangely elemental in connection with a work of that nature; but in reality it represented an expression of the most advanced thought of the period when it was issued, and to Schlotheim should be given the credit for having laid the foundation upon which

Brongniart and his contemporaries and successors erected the superstructure which gradually developed into the science of paleobotany as we now recognize it.

The first great basic fact, therefore, that paleobotany proclaimed was that our living flora had an ancestry whose elements were different from those now in existence. As facts accumulated, and the floras of the successive periods in the earth's history became better and better known, the phylogenetic development from low and simple types of vegetation to successively higher and more complex ones was demonstrated, and a rational, philosophical basis for systematic botany was established. Before that time any system of taxonomic arrangement of the vegetable kingdom was purely theoretical. Relationships were recognized, but they were often lacking in explanation; and it is significant that every real advance which has been made in taxonomy has been in accord with our constantly increasing knowledge of phylogeny. Paleobotany is thus constantly helping to solve the broad problem of the why and wherefore of our modern systematic arrangement of the vegetable kingdom and rendering it more and more truly scientific.

If certain of the apparent anomalies in modern taxonomy are critically examined in the light of paleobotanical knowledge they become anomalies no longer. As an example we may consider the case of a monotypic genus such as *Ginkgo*. It is represented by a single living species, *G. biloba* L., and its nearest affinities among living coniferae are apparently with the Taxaceae. What is the meaning of its isolation in our scheme of classification? Does it represent a recent development of a new generic type in connection with which new species are destined to be evolved in the future, or does it represent an ancient type of vegetation of which it is now the sole survivor? Paleobotany has supplied the answer to these questions by demonstrating that the genus was formerly represented by many species and that it was merely one of a number of allied genera all of which are now extinct.

The genus *Sequoia*, with its two living species, is a similar, although not quite so striking an example of generic isolation; and in the same category may be mentioned *Nelumbo*, *Liriodendron*, *Sassafras*—each represented by but two species—and *Liquidambar* by three. All of these represent vanishing generic types as evidenced by the many known fossil species in each, now entirely extinct. It was, of course, reasonable to infer that such was the case in these and other similar instances; but paleobotanical discoveries alone furnished the definite proof.

It is, however, within the domain of what we broadly designate as

the science of ecology, and especially in connection with the problems of phytogeography, that the work of paleobotanists has been of unexpected value, in furnishing explanations of many puzzling facts of modern plant distribution. In this connection we may hark back to certain of the genera already discussed taxonomically and consider them in relation to their present geographic distribution.

The genus *Liriodendron* is represented by one species in eastern and middle North America and one in eastern Asia. The two species of *Sassafras* have the same distribution. Of the two species of *Nelumbo* one has a range in America extending from New Jersey to Colombia and the other is Asiatic. What is the meaning of the occurrence of only two species representing each genus and each of the species in such widely separated regions? We can not imagine that a genus could originate two specific types independently, each one in a different part of the world, even in a single fortuitous instance; and it is almost as difficult to believe that a genus could originate in Asia and develop a single species which somehow subsequently migrated to America and there evolved into a different species, or *vice versa*. Discussions of the possibilities of evolution, mutation, and migration afforded theoretical but unsatisfactory explanations. The discoveries of paleobotany, however, supplied actual facts, and these showed that in all such instances the genera were formerly world-wide in their distribution as well as prolific in species. A single example in this connection is sufficient. Fossil remains of some twenty-five species of *Nelumbo* have been brought to light, from the United States, British America, Greenland, England, Holland, Germany, Hungary, France, Portugal, Egypt and Japan. The problem of the modern distribution of any such genus in two widely separated parts of the world, therefore, has nothing to do with any phenomena of evolution, or mutation, or migration in modern times. It is merely a matter of elimination of species in past times, throughout the intermediate regions where they formerly flourished. On the same basis may also be explained the geographic isolation of *Sequoia* with its two living species confined to a narrow belt on the western slope of the Sierras in California, and *Taxodium* with its three living species confined to the coast region of the eastern and southern United States and the northern part of Mexico. The discoveries of paleobotany have demonstrated that in past ages both of these genera included many species and that they were widely distributed. They flourished not only in similar latitudes to those in which they now occur, but also northward beyond the Arctic circle as far as exploration has been carried. The climatic conditions of the Ice Age exterminated them everywhere in the North. The mountain systems of the Eurasian

continent, extending in an east and west direction, formed barriers which prevented their migration southward and there they became extinct. In North America, however, with its mountain systems extending in a north and south direction, migration to more congenial regions was possible and here they continued to exist. Their present isolated geographic distribution was, therefore, determined long ago, by a combination of climatic changes and topographic features, and is not a modern phenomenon that can be satisfactorily explained by present conditions alone.

Incidentally it may also be pertinent to recall that the genus *Sequoia* enjoys the unique distinction of having been found in the fossil form previous to its discovery as an element in our existing flora. Cones and leaf-bearing twigs, representing what we now know as the genus *Sequoia*, were found in Europe and were described and figured (but not, of course, under the modern generic name) before the living trees on our western coast were discovered. This fact, however, can hardly be cited as an instance in which paleobotany has been of assistance to botany, inasmuch as it involves the question in nomenclature whether or not the generic name first applied to the fossil remains should have precedence over that subsequently given to the living trees.

I shall not attempt, in this paper, to discuss the debt which botany owes to those paleobotanical students who have made special studies of the internal structure of fossil plants, and thus determined exact botanical relationships along lines of modern morphological investigations. This is a relatively recent phase in the development of paleobotany and the results attained are familiar to us all. The discovery of the extinct class or order of plants, the Pteridosperms or Cycadofilicales, and its taxonomic relations to the Pteridophytes and Gymnosperms, is due to their labors, as is also the determination of the exact affinities of many extinct families and genera with those now living. They have filled in the details of the broad phylogenetic sequence outlined by the earlier paleobotanists and they represent the field of work in which botany and paleobotany are most closely and intimately related today and in which it is impossible to dissociate them.

# FURTHER NOTES ON THE STRUCTURAL DIMORPHISM OF SEXUAL AND TETRASPORIC PLANTS IN THE GENUS GALAXAURA

MARSHALL A. HOWE

*The New York Botanical Garden*

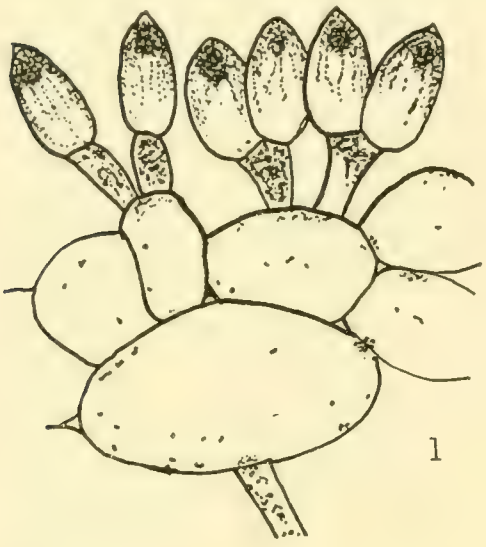
At the meeting of the Botanical Society of America, held at Columbia University in December, 1916, the writer presented a short paper, since published,[1] in which evidence was brought forward to show that *Galaxaura obtusata*, a calcified red alga of the family Chaetangiaceae, presents itself in two forms of the same general habit, but differing markedly and constantly in the microscopic structure of the cortex. In the one, the middle layer of the cortex consists chiefly of large chambers, more or less filled with lime in the natural condition, while in the other the chambers are comparatively small and the cortex is pseudoparenchymatous throughout. There are also other differences in the form and relations of the cortex cells, as pointed out in the paper to which reference has been made. In a monograph of the genus *Galaxaura*, published by Kjellman in 1900,[2] these characters were made the basis of two groups of species, denominated by him the "Cameratae" and the "Spissae." In the recently published paper, the present writer drew attention to the facts that plants showing the "Cameratae" and "Spissae" structure are commonly collected together throughout the West Indian region, that they show the same or parallel variations in external habit, that they can not, in fact, be separated without a microscopic examination, and that, whenever reproductive organs can be found, the plants of the "Cameratae" structure are always tetrasporic, while those of the "Spissae" structure are always antheridial or cystocarpic. The writer therefore expressed the conviction "that the 'Spissae' and 'Cameratae' characters, first accurately pointed out by Kjellman, do not offer a proper basis for subgeneric groupings of species as supposed by him," but merely distinguish the sexual and tetrasporic phases in the life-cycle of a single species.

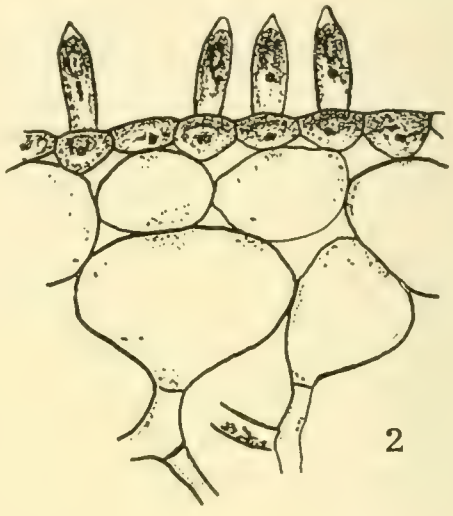
Since reading and publishing the short paper to which reference

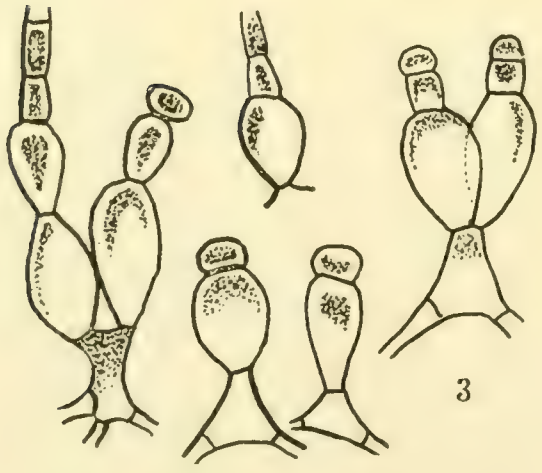
[1] Structural dimorphism of sexual and tetrasporic plants of *Galaxaura obtusata*. Bull. Torrey Club 43: 621–624. 10 Ja 1917.

[2] Kjellman, F. R. Om Floridé-slägtet *Galaxaura*, dess organografi och systematik. Kongl. Sv. Vet.-Akad. Handl. 33[1]: 1–109. *pl. 1–26.* 1900.

has been made, the writer has been investigating some of the other sections of *Galaxaura* as proposed or recognized by Kjellman in his monograph of the genus and as accepted without question by writers on the red algae during the past seventeen years, and grounds have been found for believing that a similar relation exists between several other pairs of groups hitherto considered to be independent. The



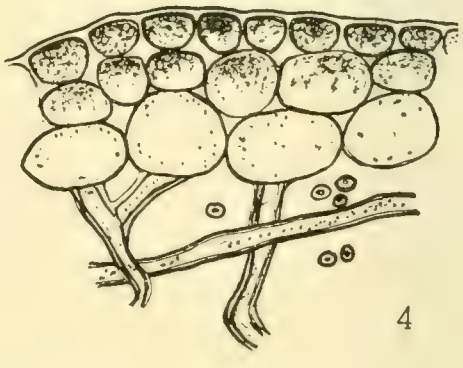




FIG. 1. Cortex of a tetrasporic plant of *Galaxaura marginata* (Ell. & Soland.) Lamour., in section, illustrating the cortex structure of the section "Brachycladia"; enlarged about 210 diameters. (After Børgesen.)

FIG. 2. Cortex of antheridial plant of *Galaxaura marginata* (Ell. & Soland.) Lamour., in section, illustrating the cortex structure of Kjellman's section "Vepreculae," enlarged about 300 diameters. (After Børgesen, under name *Galaxaura occidentalis* Børg.)

FIG. 3. Figures showing the essentially free filaments, short and long (bases only of the long), constituting the cortex of *Galaxaura flagelliformis* Kjellm., and illustrating the cortex structure of Kjellman's section "Rhodura"; enlarged about 154 diameters. (After Kjellman.)

FIG. 4. Cortex of *Galaxaura squalida* Kjellm., in section, illustrating the cortex structure of the section "Microthoë"; enlarged 210 diameters. (After Børgesen.)

evidence associating the groups "Vepreculae" and "Brachycladia" seems particularly convincing. The name "Vepreculae" was given by Kjellman to a "section" of the genus in 1900. "Brachycladia" was proposed by Sonder as a separate genus in 1853 and is recognized as an independent genus by De-Toni in his "Sylloge Algarum," though by Kjellman it is properly considered to represent a section of *Galaxaura*. In the "Brachycladia" group, the cortex is essentially filamentous, as to its two outer layers at least (TEXT-FIGURE 1), and the cells separate easily after decalcification, though forming a more or less coherent epidermis in the natural calcified condition. The outermost or superficial cells are usually oval or ellipsoid and obtuse or apiculate. In plants of the section "Vepreculae," the cortex (TEXT-FIGURE 2) may be said to be parenchymatous or pseudoparenchymatous rather than filamentous. The epidermis here consists of cells that are firmly united both before and after decalcification and these cells have their longest axis parallel to the general surface instead of at right angles to it. In some parts of the thallus, especially at the edges of the flattened branches, the surface shows few or numerous, scattered or crowded, blunt or apiculate, papilla-like cells, which are probably homologous with the outermost or epidermal cells in the "Brachycladia" section, though they do not here form the epidermis, the firmly united epidermal cells of the "Vepreculae" section being probably homologous with the widely spaced subepidermal stalk-cells of the "Brachycladia" section. Now, an examination of a wide series of plants of the "Brachycladia" structure from the West Indies, as well as an examination of the type material of nearly all of the species from various parts of the world referred to this section by Kjellman, indicates that whenever reproductive organs are found, the plants of this group are always tetrasporic, and, in the same way, plants showing the "Vepreculae" structure are always antheridial or cystocarpic. Moreover, in the West Indies, at least, the writer's personal experience in collecting shows that plants of these two types of cortex-structure often occur together and that they show the same or parallel variations in external habit. They resemble each other very much in size and habit (PLATE III; PLATE IV, FIGURE 1), but may usually be distinguished under a hand-lens, if not at sight, by differences in the texture of the epidermis, that of the "Vepreculae" being more compact and parenchymatous and often more smooth and shiny. Of the occurrence of these two forms together, three cases may be cited: In one collection (no. 6515) of 40 plants, all believed referable to *Galaxaura marginata*, found growing together just below low-water mark near Guantanamo Bay, Cuba, 26 have been examined microscopically and of these 26, 13 were of the "Brachycladia" struc-

ture and tetrasporic, 7 were of the "Vepreculae" structure and cystocarpic, 5 were of the "Vepreculae" structure and antheridial, and 1 was of the "Vepreculae" structure and apparently sterile. Of 9 plants (no. 6966) found growing together at the mouth of Guanica Harbor, Porto Rico, 6 were of the "Vepreculae" structure, 2 of them being obviously antheridial, and 3 were of the "Brachycladia" structure, 2 of them obviously tetrasporic. Of 5 specimens (no. 7468) found near low-water mark on Muertos Island, Porto Rico, 2 were of the "Brachycladia" structure and tetrasporic, and 3 were of the "Vepreculae" structure, 1 being cystocarpic, 1 antheridial, and 1 apparently sterile. In some cases, a considerable series of specimens, all of one group, has been collected, but in collecting the red algae it often happens, as is well known, that the plants found at one time and place may be either all tetrasporic or all sexual. Without waiting for the results of cultural experiments which might furnish absolutely complete proofs of the suggested genetic continuity, it seems to the writer that the evidence is overwhelming that the so-called species of the Kjellman's "Vepreculae" section are simply the sexual phases of the species of the "Brachycladia" section. It is of interest to note that Børgesen, in a recent instalment of his admirable series of papers on "The Marine Algae of the West Indies,"[3] relying upon the sectional distinctions proposed by Kjellman, appears to have described and figured the antheridial plant (sect. "Vepreculae") of *Galaxaura marginata* (Ell. & Sol.) Lamour. as a new species under the name *Galaxaura occidentalis* Børg., taking the tetrasporic plant (sect. "Brachycladia") to be the true *G. marginata*.[4]

When we come to examine the alleged species of some of the other sections of the genus *Galaxaura*, as monographed by Kjellman, we find strong evidences of other correlations similar to those already described for the Cameratae-Spissae and Brachycladia-Vepreculae groups. In Kjellman's section "Rhodura," the peripheral elements of the thallus are so manifestly and predominantly filamentous (TEXT-FIGURE 3) that there is little ground for using the term "cortex" in connection with these plants, yet there is commonly a

[3] 2: 109–113. *f. 118–123.* 1916.

[4] The original of the *Corallina marginata* of Ellis and Solander (Nat. Hist. Zooph. 115. *pl. 22. f. 6.* 1786) was from the Bahama Islands, and, like most of the Ellis and Solander types, it is not certainly known to be now in existence. However, there is, in the herbarium of the Royal Botanic Gardens at Kew, an old fragment, inscribed in the hand of Lamouroux:

Galaxaura marginata
Corallina ..... Sol. et Ell.
Bahame

which may or may not represent an authentic bit from the Ellis collection. This is antheridial and has the "Vepreculae" structure.

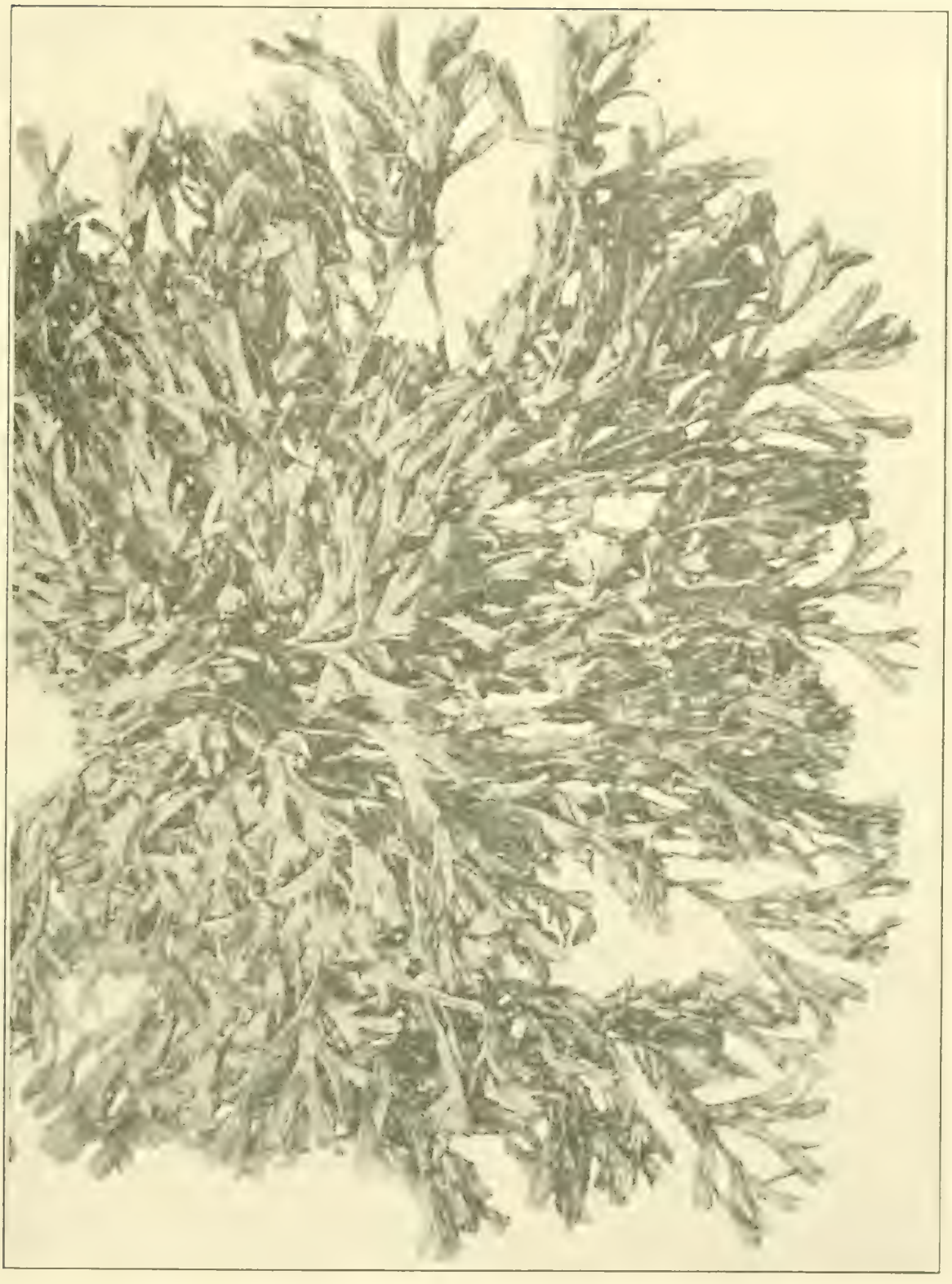
dimorphism in these peripheral assimilatory filaments, one set being long and another short, and the short ones, more or less even-topped, may sometimes be said to form a loose cortex. Whenever reproductive organs are found on plants of the "Rhodura" section, they are always tetrasporangia, never antheridia or cystocarps. In the section "Microthoë," one finds a firm, compact, pseudoparenchymatous cortex—usually firm and coherent, even after decalcification (TEXT-FIGURE 4). In some of the species or forms belonging in this section, the smooth firm epidermis bears, in certain parts of the thallus, numerous long assimilatory filaments, and, when these are particularly abundant, plants of the section "Microthoë" may look much like those of the section "Rhodura," but, generally speaking, it may be said that the firm smooth cortex of plants of the "Microthoë" section and the rough shaggy exterior of plants of the "Rhodura" section give them a very different appearance and it is no wonder that they have been considered not only as different species but also as members of different sections of the genus. But members of the "Microthoë" section, except when apparently sterile, are always either antheridial or cystocarpic—never tetrasporic—just as members of the "Rhodura" section are always tetrasporic and never sexual. And plants of the "Microthoë" section and those of the "Rhodura" section grow often so closely associated—often intertangled in the same tuft—that it seems to be a fair inference that they represent phases in the development of one and the same species. Two plants from a collection (no. 1859) of about 100 specimens made by the writer near Santurce, Porto Rico, in 1903, are shown on PLATE IV. Not all of the material in this collection has been examined microscopically, but, roughly speaking, about 80 of the 100 have the "Rhodura" structure, some of them being obviously tetrasporic and others apparently sterile; and about 20 of the 100 are of the "Microthoë" structure, some of them being obviously antheridial or cystocarpic and others apparently sterile. These plants of the "Rhodura" section appear to represent a condition of what Kjellman described as a new species under the name *Galaxaura flagelliformis*, though usually less "flagelliform" than Kjellman's original; the plants of the "Microthoë" section represent what Kjellman described as a new species under the name *Galaxaura squalida*. The two forms, as shown in FIGURES 2 and 3 (PLATE IV), differ much in habit, yet, if we consider only the lower part of the *Galaxaura squalida*, where the cortex is more or less covered with free assimilative filaments, it looks a good deal like the shaggy tetrasporic plant, *G. flagelliformis*. These Porto Rican specimens lying under the no. 1859 were collected by the writer in his less experienced and less critical days and were put together under one field number as

representing a single species, as in all probability they do, even though the current system of classification would require us to put them not only in different species-covers, but also in different sections of the genus. Likewise, in Bermuda, these two forms, *Galaxaura flagelliformis* and *G. squalida*, occur and in one instance, at least, they have been placed together under one field number by F. S. Collins (8486 in herb. N. Y. Bot. Gard.).

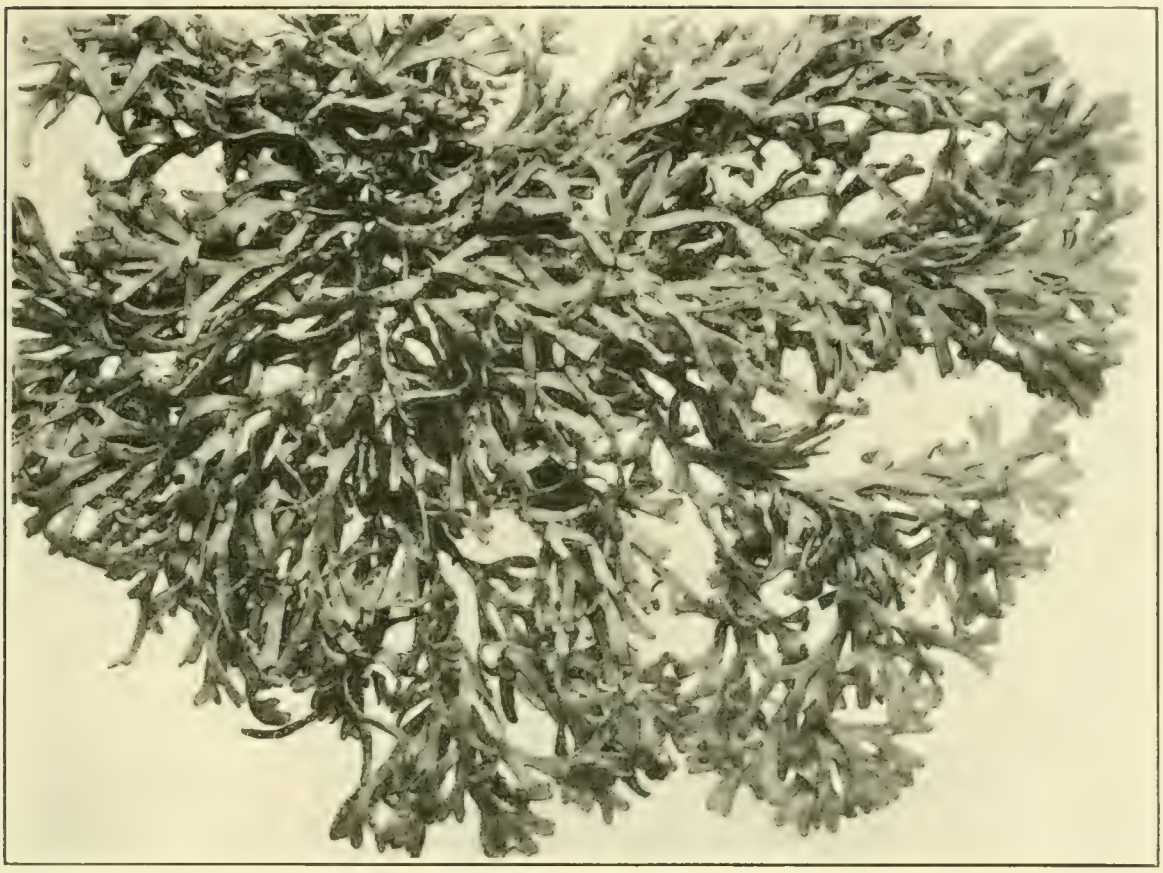
In a similar way, *Galaxaura subverticillata* Kjellm., a tetrasporic plant representing the section "Rhodura," and *G. rugosa* (Ell. & Sol.) Lamour., a sexual plant representing the section "Microthoë," are, in all probability, phases in the life-cycle of one and the same species. As instances of their occurrence together may be mentioned the writer's no. 2042 (Santurce, Porto Rico), in which the two, the *G. subverticillata* with young tetrasporangia and the *G. rugosa* with cystocarps, were found intertangled in the same tuft; the writer's nos. 7470 (*G. subverticillata*) and 7469 (*G. rugosa*), growing close together and sometimes intermingled, near the low-water line on Muertos Island (Caja de Muertos), Porto Rico; the writer's no. 4909a, *G. subverticillata*, tetrasporic, occurring with or near no. 4911, *G. rugosa*, cystocarpic, and other forms of *Galaxaura* at Montego Bay, Jamaica. It must be confessed, however, that *G. subverticillata* occurs also with sexual plants that agree more closely with *G. squalida* than with *G. rugosa* and that just as the lines of distinction between *G. flagelliformis* and *G. subverticillata* often seem vague and uncertain, so also do *G. squalida* and *G. rugosa* appear to intergrade.

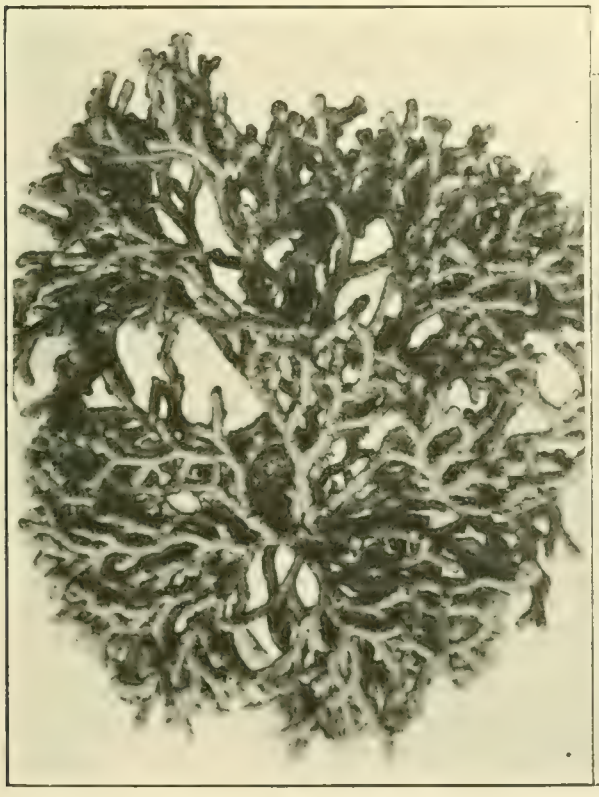
The plants included by Kjellman in his section "Eugalaxaura" appear to be all sexual, never tetrasporic. The cortex is here smooth and firm, much as in the section "Microthoë," but the epidermal cells are commonly smaller, the cortex dissolves into its constituent filaments more readily on decalcification, the thallus is more distinctly jointed, and free superficial assimilatory filaments are of less frequent occurrence. The tetrasporic phases of the "Eugalaxaura" forms are apparently to be found in the section "Rhodura," this section supplying the tetrasporic conditions for both the section "Microthoë" and the section "Eugalaxaura." From size and association (at Santurce, Porto Rico, and elsewhere) more than from any similarity in habit (for the two are, as a rule, strikingly different in habit), the writer believes that *Galaxaura cylindrica* (Ell. & Sol.) Lamour. of the section "Eugalaxaura" finds its tetrasporic phase in *G. lapidescens* (Ell. & Sol.) Lamour., of the section "Rhodura," as this species has been recently limited and defined by Børgesen.[5] And, with less assurance, it may

[5] Mar. Alg. Dan. W. I. 2: 95–99. *f. 102–104.* 1916.



Howe: Galaxaura marginata (Ell. & Soland.) Lamour. (Antheridial, Section "Vepreculae.")





HOWE: 1. GALAXAURA MARGINATA (ELL. & SOLAND.) LAMOUR. (TETRASPORIC, SECTION "BRACHYCLADIA.")

2. GALAXAURA FLAGELLIFORMIS KJELLM. (SECTION "RHODURA.")

3. GALAXAURA SQUALIDA KJELLM. (SECTION "MICROTHOË.")

be surmised that *Galaxaura oblongata* (Ell. & Sol.) Lamour.[6] has its tetrasporic condition in *G. comans* Kjellm. And just as the line of demarkation between *Galaxaura oblongata* and *G. cylindrica* seems a little uncertain and arbitrary, so also is the line of separation between *G. comans* and *G. lapidescens*. Where there is so much difference in habit as there is between the "Rhodura" forms on the one hand and the "Microthoë" and "Eugalaxaura" forms on the other, there is manifestly more need for a cultural demonstration of their correlation as alternating generations than there is in the case of the Cameratae-Spissae and Brachycladia-Vepreculae groups, where the two phases have the same outward appearance. But while experimental demonstration or further observations in the field may be desirable for a precise correlation of the "Rhodura" forms, the existing evidence that these "Rhodura" forms represent tetrasporic phases of "Microthoë" and "Eugalaxaura" forms seems convincing.

## EXPLANATION OF PLATES III AND IV

### Plate III

Photograph of a formalin-preserved antheridial specimen of *Galaxaura marginata* (Ell. & Soland.) Lamour., representing Kjellman's section "Vepreculae." Specimen from San Juan, Porto Rico (*Howe 2304*); natural size.

### Plate IV

Fig. 1. Photograph of a formalin-preserved tetrasporic specimen of *Galaxaura marginata* (Ell. & Soland.) Lamour., representing the section "Brachycladia." Specimen from San Juan, Porto Rico (*Howe 2304*); natural size.

Fig. 2. Photograph of a formalin-preserved specimen representing a form of *Galaxaura flagelliformis* Kjellm. and belonging in Kjellman's section "Rhodura." Specimen from Santurce, Porto Rico (*Howe 1859a*); natural size.

Fig. 3. Photograph of a formalin-preserved specimen of *Galaxaura squalida* Kjellm. Specimen from Santurce, Porto Rico (*Howe 1859b*); natural size.

[6] *Galaxaura fragilis* of Kjellman and of Børgesen; not *Dichotomaria fragilis* Lamarck, the type specimen of which in herb. Mus. Paris. appears to have the structure of the "Spissae" group.

# THE UREDINALES OF OREGON[1]

H. S. JACKSON

*Purdue University*

Since no account of the rusts of any of the states bordering on the Pacific coast is available for reference by the students of the flora of that region, it has seemed desirable to bring together in the form of an annotated list the results of a study of the species occurring in Oregon, which has extended, intermittently, over a period of eight years.

The account is the result of a study begun by the author in 1909 at the Oregon Agricultural College and finally prepared in the form here presented at the Purdue University Agricultural Experiment Station.

On account of the great diversity of conditions the State of Oregon presents a wonderful field for work in any phase of botanical study. The area of the State is approximately 96,000 square miles, an area considerably greater than that included in all the New England states combined. The great range of climatic and topographical features existing in the State offers favorable conditions for the development of a flora not only large in number of species, but very diverse in character. Within the confines of the State is to be found a range in altitude from sea level to perpetually snow-capped mountains. The annual rainfall varies from over 80 inches in some localities to below 10 inches in others, resulting in the development of a flora almost tropical in its luxuriance on the one hand, and one having many of the characteristics of a desert on the other.

The diversity of the Phanerogamic flora which has developed under these conditions offers an especially attractive field for the student of the parasitic fungi. Many species of all groups are to be found especially in those portions of the State having a heavy annual rainfall.

Rusts are found in great profusion in all sections of the State. The first collections of this group made by the writer were accumulated in connection with an effort to obtain general material for class use. The greater part of the collections have been made in connection with local excursions, the primary object of which was recreation.

[1] Contribution from the Botanical Department of Purdue University Agricultural Experiment Station.

Many of the collections made by the writer at localities outside of Benton County have been picked up in spare moments on trips taken in connection with Experiment Station or Extension Service duties. During 1914 and 1915, however, a number of special excursions were made primarily for collecting this group of fungi.

In addition to those made by the writer, several hundred collections made by his former associates, assistants and students at the Oregon Agricultural College are included. The greater number of these were collected by Prof. H. P. Barss, Mr. F. D. Bailey and Mr. G. B. Posey. To these have been added a considerable number of records obtained from miscellaneous sources. Several of these were obtained from the herbarium of the New York Botanical Garden, and of the National Museum. A considerable number are in the Arthur Herbarium at the Purdue University Agricultural Experiment Station. The greater number of these were obtained originally from phanerogamic specimens mainly collected and distributed by pioneer botanists of the region, particularly W. C. Cusick, Thomas Howell, J. B. Lieberg and E. P. Sheldon, E. R. Lake and others.

A few collections were made in Oregon by Dr. David Griffiths and associates, most of which were distributed in his "West American Fungi." Mr. E. Bartholomew collected at a few localities in Oregon in 1915 and distributed the specimens in the exsiccati, "Fungi Columbiani" and "North American Uredinales," which he edits. A number of specimens of rusts, the records of which were obtained mainly from the Arthur Herbarium, were made by Moses Craig, at one time botanist at the Oregon Agricultural College. It is evident that he made quite an extensive collection of rusts in Oregon, but the location of his collection at the present time is unknown to the writer.

One of the most interesting collections which it has been the privilege of the writer to examine was made by Dr. J. R. Weir, mainly in the northeastern and southwestern parts of the State. This collection consists of about 130 numbers and was sent to this laboratory for study in 1915 and 1916. Another interesting collection of about 30 numbers was made by Dr. E. P. Meinecke in southwestern Oregon and forwarded to the writer for study.

Approximately thirteen hundred collections have been examined in the preparation of this account and are listed in the following pages. By far the greater number of these, about one thousand, were made in western Oregon, including the Cascade Mountains. Of this number about six hundred were made in the Willamette Valley, four hundred having been collected in Benton County, mostly in the vicinity of Corvallis. Two hundred and fifty are listed from the Cascade mountain region, most of the collections having been made in the vicinity

of Mt. Jefferson or in Hood River County. About sixty collections are recorded from the counties bordering on the coast, only a few of which are from the southern coast counties. Less than three hundred collections have been made in eastern Oregon, almost half of which are from the mountainous region of the northeastern part.

It will be seen from the above summary of the distribution of the collections recorded that only a very small portion of the State has been explored for this group of fungi. Much remains to be done, particularly in southwestern Oregon and in eastern Oregon. The mountains of the Coast Range have been explored only in Benton County, where several collections have been made on Mary's Peak. The coast counties also offer a rich field for the collector. The region around Corvallis in Benton County is the only portion of the State that can be said to have been carefully explored for rusts. Corvallis is situated at the junction of the Willamette River and Mary's River and lies in the edge of the foothills of the Coast Range.

In spite of the fact that the exploration so far conducted is inadequate to furnish a very accurate idea of the rust flora of the State, records for 220 species are brought together in the account which follows. These occur on about 500 different host plants. In connection with the study of the collections 10 species have been found which are believed to be new to science, 8 of which are described in the following pages. A number of European species not previously recorded for North America have also been collected in the State. A large number of unrecorded host plants have been encountered.

The number of species of economic importance found in the State is worthy of mention. All of the grain rusts recorded for North America with the exception of the corn rust (*Puccinia Sorghi*) are known to occur in the State, including the recently discovered *Puccinia glumarum*. All of the rusts troublesome to florist's crops in the greenhouse, including *Puccinia Antirrhini*, are known to occur. The Pacific coast rust of pears and quinces promises to become of considerable economic importance. The large number of forest-tree rusts found in the State offers an especially attractive field for investigation. Many heteroecious species are known to occur whose life history is not yet determined. The rusts occurring on *Salix* are especially in need of investigation.

In the notes given in connection with the account of the species which follows, an effort has been made to summarize the available information on the life history as shown by any culture work which may have been conducted either by American or European authors. Notes on the distribution in North America are given whenever it was considered of sufficient importance. The genera are listed alpha-

betically under each family and the species similarly under the genus. The host plants are also arranged alphabetically under each species.

No attempt has been made to give a full list of synonyms. In general, however, sufficient synonymy is given to show the origin of the specific name used as well as any names which have been in general use. For convenience of reference the specific nomenclature used is that in use in this laboratory, and in general conforms to that used in the "North American Flora." For similar reasons the generic nomenclature follows that proposed by Dr. Arthur, for use in the "North American Flora," except that *Melampsora*, *Puccinia* and *Uromyces*, are retained. In order to follow this system consistently it has been found necessary to establish a number of new combinations.

Under each host is given a list of the specimens examined, with locality, county, date and collector, followed by the collector's number. Numbers between 1000 and 3450 refer to collections in the Oregon Agricultural College Herbarium, if made by members of the botanical staff or by students. If no collector is given it may generally be assumed that the collection was made by the writer. In order to prevent unnecessary repetition, Benton County is not cited following collections made at Corvallis and Philomath. Similarly Hood River County is implied for all collections from Hood River or Mt. Hood and all collections made at Portland are from Multnomah County.

The writer is under great obligations to all those who have contributed specimens for study and especially to those whose names have been mentioned previously. He is also greatly indebted to those botanists who have given so generously of their time in determining host plants. Dr. A. S. Hitchcock and Mrs. Agnes Chase have named most of the grasses. Dr. Theo. Holm and Dr. K. K. Mackenzie have each determined a considerable number of species of *Carex*. Dr. C. R. Ball has named most of the willows. Dr. F. V. Coville and Dr. K. M. Wiegand have each determined several specimens of *Juncus*. Mr. Paul Standley has determined a large number of specimens from miscellaneous families.

Dr. J. C. Arthur and his former associates very kindly determined a considerable number of specimens of the rusts occurring on grasses and sedges, and verified the determinations of others, which the writer sent from Oregon at various times during the period when the collections were being made. The greater part of the collections recorded, however, have been worked over since the writer took charge of the work of this laboratory. During this period it has been his privilege to be able to consult freely with Dr. Arthur and to have the unrestricted use of the collections, catalogues, and manuscript notes on the rusts, which have been accumulated at the Purdue University

Agricultural Experiment Station during the many fruitful years of Dr. Arthur's administration of the department of botany. Without this assistance the preparation of this account in the form presented would not have been possible and the writer takes great pleasure in acknowledging his indebtedness to Dr. Arthur and to the various assistants in this laboratory for any help which they may have given.

## COLEOSPORIACEAE

1. **Coleosporium Adenocaulonis** sp. nov.

O. and I. Pycnia and aecia unknown.

II. Uredinia hypophyllous, few, scattered on conspicuous angular yellowish spots, small, 0.1–0.2 mm. across, early naked, orange yellow fading to whitish, becoming pulverulent, ruptured epidermis conspicuous; urediniospores globoid to ellipsoid, 18–24 by 23–26 $\mu$, wall light golden brown or colorless, 2–3 $\mu$ thick, prominently and moderately verrucose; pores indistinct.

III. Telia unknown.

On Carduaceae:

*Adenocaulon bicolor* Hook.—Corvallis, Sept. 20, 1914, *1549*.

This species is very inconspicuous, developing very small sori on the under side of the leaves on yellowish spots.

2. Coleosporium Madiae Cooke, Grevillea 7: 102. 1879.

On Carduaceae: II, III.

*Madia citriodora* Greene—Mary's Peak, Benton Co., Aug. 15, 1914, *1514*.

*Madia exigua* (Sm.) Greene—Corvallis, July 29, 1914, *1475;* Philomath, Aug. 15, 1914, *1516*.

*Madia glomerata* Hook.—Corvallis, Aug., 1889, E. R. Lake, July, 1910, *1159*, July 29, 1915, *3241;* Portland, Aug. 24, 1915, E. Bartholomew, *5964* (Barth. Fungi Columb. *4910*).

*Madia racemosa* (Nutt.) T. & G.—Corvallis, July, 1910, *1160*, Sept. 12, 1910, *1928;* Wren, Benton Co., June 26, 1914, *1316*, *1317*, *1322*, *1328;* Elk City, Lincoln Co., Aug. 20, 1914, *2538;* Philomath, May 10, 1914, *3246*.

*Madia ramosa* Piper—Corvallis, July 29, 1914, *1470*.

*Madia sativa* Molina—Corvallis, Aug. 12, 1910, *1163*, July 29, 1914, *1474*.

The aecial connection of this very common species has not been demonstrated by cultures and no field observations have been made in Oregon. Judging from distributional data, however, it seems probable that *Peridermium californicum* Arth. & Kern may be genetically connected.

From field observations made by the writer it is evident that in western Oregon this species overwinters in the uredinial stage.

3. Coleosporium occidentale Arth. North American Flora 7: 94. 1907.

On Carduaceae: II.

*Senecio triangularis* Hook.—Mary's Peak, Benton Co., Aug. 15, 1914, *1518*.

This species is known otherwise only from the type collection made in Falcon Valley, Washington, on *S. hydrophiloides* Rydb., by W. N. Suksdorf in 1900.

The aecial connection is not known and no clues are available. The aecia, in common with other species of *Coleosporium* whose life history is known, should be looked for on the leaves of *Pinus* sp. The above collection, however, was made in a region where no pines exist in a radius of several miles. It is probable that this species, in common with some other members of the genus, is capable of being carried over the winter in the uredinial stage.

The only pine-leaf-inhabiting *Peridermium* known to the writer in the present range of this species is *P. montanum* Arth. & Kern, which has been shown to be genetically connected with a *Coleosporium* on *Aster* and *Solidago*, referred to *C. Solidaginis*.

4. Coleosporium Solidaginis (Schw.) Thüm. Bull. Torrey Club 6: 216. 1878.

*Uredo Solidaginis* Schw. Schr. Nat. Ges. Leipzig 1: 70. 1822.

*Peridermium acicolum* Und. & Earle, Bull. Torrey Club 23: 400. 1896.

*Peridermium montanum* Arth. & Kern, Bull. Torrey Club 33: 413. 1906.

On Pinaceae: I.

*Pinus contorta* Dougl.—North slope Mt. Hood, Aug. 7, 1914, *1610*.

On Carduaceae: II, III.

*Aster conspicuus* Lindl.—Hilgard, Union Co., July 10, 1914, *1532;* Austin, Grant Co., Aug. 1915, J. R. Weir, *159*.

*Aster Cuseckii* Gray?—Corvallis, Sept. 21, 1914, *1548*.

*Aster Douglasii* Lindl.—Hood River, Aug. 26, 1915, E. Bartholomew, *5972* (Barth. Fungi Columb. *4911*); Corvallis, June 29, 1914, G. B. Posey, *1310*.

*Aster foliaceus frondeus* Gray—Hood River, July 22, 1915, *3137;* Clatskanie, Columbia Co., May 20, 1914, F. D. Bailey, *2564*, Oct. 29, 1914, *2531;* Corvallis, June 29, 1914, G. H. Godfrey, *1307*.

*Aster Hallii* Gray—Corvallis, July 29, 1914, *1471;* Wren, Benton Co., July 26, 1914, *1318*.

*Solidago caurina* Piper—North slope Mt. Hood, Aug. 7, 1914, *1605*.

*Solidago elongata* Nutt.—Corvallis, July 29, 1915, *3244;* Scotts, 7 miles N. of Fort Klamath, Klamath Co., Sept. 20, 1913, E. P. Meinecke, *Cr D 7*.

*Solidago missouriensis* Gray?—Sumpter, Baker Co., Aug. 21, 1915, J. R. Weir, *267*.

*Solidago tolmieana* Gray?—Hood River, July 23, 1915, *3254*.

The life history of this species was first demonstrated by Clinton (Science N. S. **25**: 289. 1907; Ann. Rep. Conn. Exp. Sta. **1906**: 320. 1907; **1907**: 375. 1908). He successfully infected *Solidago rugosa* with aeciospores of *Peridermium acicolum* on *Pinus rigida*.

The single collection of aecia listed above (1610) agrees with the description of *P. montanum* Arth. & Kern and was collected in the immediate vicinity of *Solidago caurina* (1605). The possibility of genetic relationship was made note of at that time. Hedgcock (Mycologia **4**: 144. 1912; Phytopath. **3**: 16. 1913) has also made similar observations and more recently (Phytopath. **6**: 65. 1916) has cultured this *Peridermium* successfully on *Aster conspicuus*, using aecial material on *Pinus contorta* collected in Montana. Weir and Hubert (Phytopath. **6**: 68. 1916) working independently from Hedgcock, with similar aecial material, have also demonstrated by cultures that this *Peridermium* has its uredinia on both *Aster* and *Solidago*, having obtained infection on *A. laevis geyeri*, *S. canadensis* and *S. missouriensis*.

Sydow (Monographia Ured. **3**: 621. 1915) suggests that the form on *Aster* in North America is different from *C. Solidaginis* on *Solidago* and should either be united with the Asiatic *C. Asterum* (Diet.) Syd. or that it represents an unrecognized species having a different *Peridermium* as its aecial form. The culture work of Weir and Hubert (l. c.), however, shows that *P. montanum* is genetically connected with uredinia on both *Aster* and *Solidago* and does not lend support to Sydow's view.

While the two species of *Peridermium* included here are widely separated as to range and are morphologically distinguishable, it seems best until further culture work is conducted to recognize but one American species.

## UREDINACEAE

5. Calyptospora columnaris (Alb. & Schw.) Kühn; Rab.-Wint. Fungi Eur. 3521. 1886. (Hedwigia **26**: 28. 1887.)

*Aecidium columnare* Alb. & Schw. Consp. Fung. 121. 1805.

*Calyptospora Geoppertiana* Kühn, Hedwigia **8**: 81. 1869.

On Pinaceae: I.

*Abies grandis* Lindl.—Scottsburg, Lane Co., Sept. 1, 1914, G. G. Hedgcock, *20210.*

*Abies magnifica* A. Murr.—Road to Crater Lake, Union Creek, Camp Grant, Klamath Co., Sept. 23, 1913, E. P. Meinecke, *Cr D 20.*

On Vacciniaceae: III.

*Vaccinium macrophyllum* (Hook.) Piper—Austin, Grant Co., June, 1913, J. R. Weir, *25;* Sumpter, Baker Co., June, 1913, J. R. Weir, *24;* Silver Creek, Josephine Co., July 28, 1913, E. P. Meinecke, *S1 (D6) D1.*

*Vaccinium myrtilloides* S. Wats.—Road to Crater Lake, Union Creek to Camp Grant, Klamath Co., Sept. 23, 1913, E. P. Meinecke, *Cr D 19.*

*Vaccinium ovalifolium* Smith—Larch Mt., Multnomah Co., Aug. 1910, *1156;* North slope Mt. Hood, Aug. 7, 1914, *1608.*

*Vaccinium ovatum* Pursh—Dothan, Douglass Co., Sept. 8, 1914, G. B. Posey, *1932;* Waldo, Josephine Co., Sept. 5, 1916, J. R. Weir, *280;* Oregon, April 19–31, 1911, H. D. House.

*Vaccinium parviflorum* Smith—Whitewater Ranger Station, near Mt. Jefferson, Aug. 12, 1914, H. P. Barss & G. B. Posey, *1750.*

*Vaccinium scoparium* Lieb.?—Mary's Peak, Benton Co., Aug. 15, 1914, *1284.*

Specimens of aecia collected in various parts of North America on *Abies balsamea, A. concolor* and *A. lasiocarpa* are now referred to this species in the Arthur herbarium.

The life history was first demonstrated by Hartig (Allg. Forst.- u. Jagdzeitg. 289. 1880), who conducted culture investigations using aecia on *Abies pectinata* and telia on *Vaccinium Vitis-idaea.* He obtained successful infection in both directions. Other European investigators, notably Dr. G. Winter, have amply confirmed these results. (Klebahn, Die Wirtsw. Rostpilze 391. 1904.)

In America, Arthur (Mycologia **2**: 231. 1910) was the first to culture this species and succeeded in obtaining aecia on *Abies Fraseri* following exposure to infection from telia on *Vaccinium pennsylvanicum* sent by W. P. Fraser from Nova Scotia. Later in the same year Fraser made the first field collection of aecia on *Abies balsamea* (Science **30**: 814. 1909) and later (Mycol. 4: 177. 1912; 6: 27. 1914) confirmed Arthur's work by obtaining infection on *Abies balsamea* from telia on *Vaccinium pennsylvanicum.*

6. Chrysomyxa Weirii Jackson, Phytopath. 7: 353. 1917.

On Pinaceae:

*Picea Engelmanii* Parry—Whitman Nat. Forest, Oregon, July 17, 1913, J. R. Weir, *271.*

This species differs from *C. Abietis* in the narrower, somewhat smaller spores which do not long remain in chains but soon break apart. No evidence of germination has been seen in any of the collections. This is the only American representative of the genus as restricted by Arthur. (Result Sci. Congr. Bot. Vienne 338. 1906.) It is known to the writer otherwise only from single collections from British Columbia and Idaho. It is doubtless not uncommon in the northwest.

7. Cronartium filamentosum (Pk.) Hedgcock, Phytopath. 2: 177. 1912.

*Peridermium filamentosum* Pk. Bot. Gaz. 7: 56. 1882.

*Uredo coleosporioides* Dietel & Holway, Erythea 1: 247. 1893.

*Peridermium stalactiforme* Arth. & Kern, Bull. Torrey Club 33: 419. 1906.

*Cronartium coleosporioides* Arth. N. Am. Flora 7: 123. 1907.

On Pinaceae: I.

*Pinus contorta* Dougl.—Scotts, Anna Creek, Klamath Co., May 23, 1912, E. P. Meinecke, used for inoculation on *Castilleja miniata;* Gold Center, June 20, 1914, H. F. Wilson, *1856;* North slope Mt. Hood, elev. 3,000–4,000 ft.; Aug. 7, 1914, *3332;* Sumpter, Baker Co., May, 1916, J. R. Weir.

On Scrophulariaceae: II, III.

*Castilleja* sp.—North slope Mt. Hood, 3,000–4,000 ft., Aug. 7, 1914, *1612, 1615* (collected near *3332*); Ashland Toll House, Jackson Co., Sept. 27, 1913, E. P. Meinecke, *Cr D 22.*

Hedgcock (l. c.) was the first to publish a record of connection of *Peridermium filamentosum* with a *Cronartium* on *Castilleja* by cultures. He considered this distinct, however, from *Cronartium coleosporioides,* which Meinecke had cultured in 1911 (Phytopath. 3: 167–168. 1913) and shown to have for its aecial form *P. stalactiforme.* Meinecke's culture material was collected in Klamath Co., Oregon.

Further culture work has been carried on by Weir and Hubert (Jour. Agr. Research 5: 781–785. 1916) in which it is shown that the gall-forming *Peridermium* on *Pinus contorta* which has previously been commonly referred to *P. Harknessii* Moore is but a form of *P. filamentosum.*

All the records of the aecial stage given above are of the gall-forming type. The Hood River material was collected in the immediate vicinity of the telial form on *Castilleja.*

8. Cronartium pyriforme (Pk.) Hedgc. & Long, Alt. Stage Peridermium pyriforme 3, 1914.

*Peridermium pyriforme* Peck, Bull. Torrey Club 6: 13. 1875.

*Cronartium Comandrae* Peck, Bull. Torrey Club **11**: 50. 1884.

*Peridermium Betheli* Hedgc. & Long, Phytopath. **3**: 251. 1913.

On Pinaceae: I.

*Pinus ponderosa* Dougl.—Hood River Co., May 10, 1910, *3333;* Sumpter, Baker Co., May, 1916, J. R. Weir.

On Santalaceae: II, III.

*Comandra umbellata* (L.) Nutt.—Corvallis, June 20, 1909, E. R. Lake, *3068*, July 24, 1914, *2510*, Road to Ashland toll house, Jackson Co., Sept. 27, 1913, E. P. Meinecke, *Cr D 23;* Hood River Co., June 20, 1914, *1995*, July 22, 1915, *3143;* Dufur, Wasco Co., June 30, 1914, *1337;* Indian Creek, Malheur Co., Sept. 16, 1897, E. P. Sheldon, *8934*.

The collection of aecia on *Pinus ponderosa* made at Hood River consisted of a large fusiform gall at the base of the trunk of a young tree about 2 inches in diameter. The gall entirely encircled the tree which was noticeably stunted from the effects of the parasite. The foliage also showed a distinct yellow cast.

The life history of this common and widespread species was first demonstrated by Hedgcock and Long (l. c.). They succeeded in obtaining the development of uredinia on *Comandra umbellata* by exposing them to infection from aecia on *Pinus ponderosa* collected in Washington and California and on *Pinus pungens* from Pennsylvania. In a later publication the authors (Bull. U. S. Dept. Agr. **247**: 1–20. 1915) discuss the economic importance of this fungus as a disease of pines and record in detail the results of extensive culture work.

9. Hyalopsora Aspidiotus (Peck) Magn. Ber. Deuts. Bot. Ges. **19**: 582. 1901.

*Uredo Aspidiotus* Pk. Ann. Rept. N. Y. State Mus. **24**: 88. 1872.

On Polypodiaceae:

*Phegopteris Dryopteris* (L.) Fée—Austin, Grant Co., Aug. 1915, J. R. Weir, *164*.

10. Hyalopsora laeviuscula (D. & H.) Arth. North Am. Flora **7**: 113. 1907.

*Uredo laeviuscula* Dietel & Holway, Erythea **2**: 127. 1894.

On Polypodiaceae:

*Polypodium occidentale* (Hook.) Maxon—Vicinity of Mt. Jefferson, July 27, 1907, E. R. Lake, *2508;* Corvallis, March 25, 1915, G. B. Posey, *2626;* Hood River Co., May 16, 1915, *3042;* Bridal Veil, Multnomah Co., May 18, 1915, *3025*.

*Polystichum munitum* (Kaulf.) Presl., Mary's Peak, Benton Co., Apr. 23, 1915, G. B. Posey, *3041*.

The urediniospores in this species are smooth in all collections as shown by very careful examination with the oil immersion objective.

This species has not previously been recorded on the latter host so far as the writer is aware.

11. Hyalopsora Polypodii (DC.) Magn. Ber. Deuts. Bot. Ges. 19: 582. 1901.

*Uredo Polypodii* DC. Fl. Fr. 6: 81. 1815.

On Polypodiaceae:

*Filix fragilis* (L.) Underw.—Road to Lost Lake, Hood River Co., July 24, 1915, *3024*.

12. Melampsora sp.

II. Uredinia amphigenous, chiefly epiphyllous, scattered or occasionally gregarious, round, 0.5–1 mm., early naked, somewhat pulverulent, orange fading to yellowish, ruptured epidermis not conspicuous;. uredospores ellipsoid or obovoid, 15–19 by 21–24 $\mu$, wall colorless, uniformly 2.5–3 $\mu$ in thickness, moderately to closely verrucose-echinulate; paraphyses numerous, chiefly peripheral, clavate or occasionally capitate, 18–26 by 45–70 $\mu$, wall colorless, usually uniformly 1–2 $\mu$ thick, occasionally thickened at apex to 4 $\mu$.

On Salicaceae:

*Populus alba* L.—Sheridan, Yamhill Co., July 7, 1914, H. P. Barss, *1935;* Cottage Grove, Lane Co., July 17, 1914, *1933;* Philomath, July 20, 1915, *3309*.

The only other American collection on this host known to the writer is one in the Arthur herbarium, collected by E. Bethel, Aug. 7, 1913, at San Jose, Cal. These specimens differ from all other North American collections on *Populus*. It seems most probable that this is an introduced European species. Only uredinia are present in American collections and it is quite impossible to assign it to any known species without telial material. A description of the uredinial stage drawn up from the Oregon collections is given for the benefit of those who may have occasion to study this form.

The Oregon collections were all made from low, rapidly growing water sprouts.

13. Melampsora albertensis Arth. Bull. Torrey Club 33: 517. 1906.

*Caeoma occidentalis* Arth. Bull. Torrey Club 34: 591. 1907.

On Pinaceae: I.

*Pseudotsuga mucronata* (Raf.) Suds.—Southeast Mt. Jefferson, Linn Co., July 3, 1914, F. D. Bailey, *1841;* Sumpter, Baker Co., July 20, 1913, J. R. Weir, *275;* Corvallis, June 1910.

The life history of this species has been studied by Arthur (Mycologia 4: 29 and 59, 1912), who obtained infection resulting in pycnia

and aecia on *Pseudotsuga* by exposing the foliage to infection from germinating telia on *Populus tremuloides* collected in Colorado. Out of four trials, three were successful. No infection was obtained on *Larix*.

It is noteworthy in this connection that all of the northwestern collections have larger spores than specimens from Colorado. The former show spores 20–28 by 24–32 μ while the average of the latter are 16–20 by 19–26 μ. The culture work was conducted with Colorado material, nearly if not all of which was collected in immediate association with *M. albertensis* on *P. tremuloides*. The type of *Caeoma occidentale*, on the other hand, was collected in British Columbia and has larger spores. It seems entirely possible that the northwestern collections may represent a different species and have genetic relationship with some form on *Populus* other than *M. albertensis*.

14. Melampsora arctica Rostr. Medd. Grönland 3: 535. 1888.

On Salicaceae:

*Salix Bebbiana* Sarg.—Sumpter, Baker Co., Aug. 1915, J. R. Weir, *167*.

*Salix fendleriana* And.—Sumpter, Baker Co., June, 1913, J. R. Weir, *8*.

*Salix lutea* Nutt.—Sumpter, Baker Co., June, 1913, J. R. Weir, *4*.

*Salix sitchensis* Sanson—Dothan, Douglass Co., Sept. 8, 1914, G. B. Posey, *3342*.

*Salix* sp.—Scott's, 7 miles from Fort Klamath, Klamath Co., Sept. 20, 1913, E. P. Meinecke, *Cr D 6*.

It is with considerable hesitation that the above collections have been referred to this species. Only those collections which have small, rather thin-walled uredospores, accompanied by an abundance of thin-walled, clavate paraphyses, are included.

Fraser, working with material collected in Nova Scotia (Mycol. 4: 187. 1912; 5: 238. 1913), has made a cultural study of this species. He succeeded in obtaining infection on *Abies balsamea* with production of pycnia and aecia following exposure to germinating telia from *Salix discolor*.

15. Melampsora Bigelowii Thüm. Mitth. Forstl. Vers. Oest. 2: 37. 1879.

On Pinaceae: I.

*Larix occidentalis* Nutt.—Hood River Co., elevation 4000°, July 23, 1915, *3305*, *3365*.

On Salicaceae: II, III.

*Salix Bebbiana* Sarg.—Austin, Grant Co., Aug. 1915, J. R. Weir, *162*, *163;* Sumpter, Baker Co., July 19, 1913, J. R. Weir, *272*.

*Salix cordata* Muhl.—Sumpter, Baker Co., Aug. 1915, J. R. Weir, *167*.

*Salix Piperi* Bebb.—Philomath, Oct. 29, 1911, *3346;* The Dalles, Wasco Co., Aug. 26, 1915, E. Bartholomew (Barth. Fungi Columb. *4736*).

*Salix pseudocordata* Anders.—Hilgard, Union Co., July 10, 1914, *1536*.

*Salix scouleriana* Barr.—Corvallis, Sept. 19, 1910, *1165;* St. Johns, Multnomah Co., June 23, 1915, W. E. Lawrence, *3347;* Austin, Grant Co., Aug. 1915, J. R. Weir, *165;* Portland, Aug. 24, 1915, E. Bartholomew (Barth., N. Am. Ured. *1417*).

*Salix* sp.—Calamity, Aug. 1901, Griffiths & Morris (Griffiths, W. Amer. Fungi *341*); Crater Lake, Klamath Co., Sept. 22, 1913, E. P. Meinecke, *Cr Pk D* (*2*) *13;* Hood River Co., May 14, 1914, *1509*, Aug. 5, 1914, *1483*, *1484;* Beaverton, Washington Co., July 15, 1914, F. D. Bailey, *1507;* Austin, Grant Co., Aug. 25, 1915, J. R. Weir, *262*.

The above specimens are tentatively assigned to this species. There are quite certainly not less than four species of *Melampsora* on *Salix* in North America. The characteristics by which they may be separated in the uredinial stages are not well worked out at the present time. The larger spored forms have been included here under *M. Bigelowii*.

Arthur (Jour. Myc. **11**: 60. 1905) first established the fact that this rust has its aecia on *Larix*. He succeeded in infecting *Larix decidua* in two trials, by inoculating with basidiospores from germinating telia on *Salix amygdaloides* collected in Wisconsin. This result was later confirmed (Jour. Myc. **13**: 194. 1907) with telial material collected in Indiana.

Weir and Hubert (Phytopath. **6**: 372. 1916) have succeeded in obtaining infection of this species from *Salix bebbiana* Sarg. collected in Montana on *Larix occidentalis*, and from *S. cordata mackenzieana* collected in Idaho on *Larix europea*. The same authors (Phytopath. **7**: 109. 1917) have recently repeated the work with the last-named species of *Salix* and obtained infection with development of pycnia and aecia on both *L. occidentalis* and *L. europea*.

16. **Melampsora confluens** (Pers.) comb. nov.

*Uredo confluens* Pers. Obs. Myc. **1**: 98. 1796.

On Grossulariaceae: I.

*Ribes lacustre* (Pers.) Poir.—Philomath, May 3, 1913, F. D. Bailey, *1107*.

On Salicaceae: II, III.

*Salix argophylla* Nutt.—Freewater, Umatilla Co., June 17, 1913, F. D. Bailey, *1164*, Aug. 12, 1915, F. D. Bailey, *3344*.

*Salix scouleriana* Barr.—Cascade Locks, Hood River Co., Aug. 11, 1910, *1178;* Myrtle Creek, Douglass Co., June 9, 1914, F. D. Bailey, *3345;* Hood River Co., July 23, 1915, *3343, 3366;* Ashland, Jackson Co., Sept. 10, 1914, *3340, 3341.*

*Salix* sp.—Scott's, 7 miles north of Fort Klamath, Klamath Co., Sept. 20, 1913, E. P. Meinecke, *Cr D 4, Cr D 9;* Austin, Grant Co., Aug. 25, 1915, J. R. Weir, *263;* Grant's Pass, Josephine Co., Sept. 3, 1916, J. R. Weir, *266;* White Pine, Baker Co., July 20, 1913, J. R. Weir, *270;* Unity, Baker Co., Aug. 1915, J. R. Weir, *278.*

It is impossible to assign with any degree of certainty the collections which should be referred to this combination. Only those collections having small, rather thick-walled spores, accompanied by an abundance of capitate, thick-walled paraphyses, are included. It is possible that some of the collections included under *M. Bigelowii* should be referred here.

No culture work has been conducted in America. A summary of European work has been made by Klebahn (Die Wirtsw. Rostpilze 424. 1904).

In addition to the above, aecia have been collected in America on *Ribes saxosum* from Utah, *R. vallicola*, Colorado, and *R. lacustre*, British Columbia.

17. Melampsora Lini (Pers.) Desmaz. Pl. Crypt. (Fasc. 41) 2049. 1850.

*Uredo miniata Lini* Pers. Syn. Fung. 216. 1901.

On Linaceae:

*Linum Lewisii* Pursh—Blue Mts., 7,000–8,000 ft., eastern Oregon, 1897 (from phanerogamic specimen in Gray Herb. Harvard Univ.); Hermiston, Umatilla Co., May 12, 1915, *2664.*

Arthur (Jour. Myc. 13: 207. 1907) has shown this species to be autoecious. He sowed basidiospores from *Linum usitatissimum* on the same host and on *L. Lewisii* and obtained the development of pycnia and aecia.

18. Melampsora occidentalis Jackson, Phytopath. 7: 354. 1917.

On Salicaceae: II, III.

*Populus trichocarpa* Nutt.—Corvallis, Sept. 1909, *1069,* Oct. 15, 1912, *1024* (type), March 12, 1916, G. B. Posey; Trail to Sulphur Springs, Benton Co., Nov. 2, 1914, *3369;* Scott's, N. of Fort Klamath, Klamath Co., Sept. 20, 1913, E. P. Meinecke, *CrD2;* Clatskanie, Columbia Co., Oct. 6, 1914, F. D. Bailey, *3358,* Oct. 29, 1914, F. D. Bailey, *3306;* Sumpter, Baker Co., Aug. 21, 1915, J. R. Weir, *265;* Medical Springs, Union Co., Aug. 1913, J. R. Weir, *117.*

This species differs from all other species of *Melampsora* on *Populus*

in the large size of the urediniospores which are only slightly flattened and are evenly verrucose-echinulate. The teliospores are much longer than those of *M. Medusae* and are thickened at the apex. The character of the telial sori suggests that this species may be closely allied to *M. albertensis*. The sori are much larger as are also both uredinio- and teliospores.

This species may be the same as that recently cultured by Weir and Hubert (Phytopath. 7: 108. 1917), who used telial material from *P. trichocarpa* referred to *M. Medusae* and obtained successful infection on *Larix europea* and *L. occidentalis*. The actual material used for infection and the aecia resulting have not been seen by the writer but telial material sent by Dr. Weir from Montana agrees with the form described above. Aecia from the same locality on *L. occidentalis* agree in general with aecia of *Melampsora Medusae* and *M. Bigelowii*. The walls of the aeciospores are however somewhat thinner, 1–2 $\mu$, and considerably thickened on opposite sides to 3–5 $\mu$. They measure 17–19 by 19–26 $\mu$. Additional culture work, and a careful comparison of the resulting aecia with those of *M. Medusae* would be desirable. In any case, the morphological characters of the uredinial and telial stages are considered sufficient to warrant separation.

19. **Melampsora Piscariae** sp. nov.

O. and I. Pycnia and aecia unknown.

II. Uredinia hypophyllous, scattered, rounded, 0.3–0.5 mm. across, early naked, somewhat pulverulent, orange yellow fading to whitish, ruptured epidermis conspicuous; urediniospores globoid to ellipsoid, 14–16 by 16–19 $\mu$; wall colorless, 1.5–2 $\mu$ in thickness, finely and closely verrucose-echinulate; paraphyses numerous, intermixed with the spores, capitate, smooth or with an occasional conical echinulate marking, 32–64 $\mu$ long; heads 12–18 $\mu$ broad, wall uniformly thick, 2.5–4 $\mu$.

III. Telia not seen.

On Euphorbiaceae:

*Piscaria setigera* (Hook.) Piper (*Eremocarpus setigerus* Benth.)—Corvallis, Sept. 20, 1914, *3308*, type.

Known only from the type locality.

This species is referred to the genus *Melampsora* with considerable confidence in spite of the absence of telia, on account of the structure of the sorus, the character of the spores, and the presence of scattered capitate paraphyses.

20. Melampsorella elatina (A. & S.) Arthur, N. Amer. Flora 7: 111. 1907.

*Aecidium elatinum* Alb. & Schw. Consp. Fung. 121. 1805.

*Melampsorella Cerastii* (Pers.) Schroet. Krypt. Flor. Schles. $3^1$: 366. 1887.

On Pinaceae: I.

*Abies grandis* Lindl.—Mary's River, west of Wren, Benton Co., Aug. 2, 1914, *1297;* Sumpter, Baker Co., July 20, 1913, J. R. Weir, *276.*

*Abies lasiocarpa* (Hook.) Nutt.—Crater Lake, Klamath Co., Sept. 9, 1916, J. R. Weir, *209;* Sumpter, Baker Co., July, 1913, J. R. Weir, *274.*

On Caryophyllaceae: II, III.

*Cerastium vulgatum* L.—Corvallis, May 1, 1915, *2667.*

*Cerastium viscosum* L.—Corvallis, June 28, 1915, *3019.*

*Stellaria borealis* Bigel.—Corvallis, April 5, 1914, *1287.*

This rust, which is doubtless common throughout the state, is remarkable in that both stages develop from a perennial mycelium. The aecial stage forms large or small witches' brooms on the branches of various species of *Abies*, each leaf of which bears the conspicuous aecia in two rows on the under surface of the leaves.

The life history was first worked out by Fischer (Zeitschr. für Pflanzenkr. 11: 321. 1901) and has been amply confirmed by other European investigators. A summary of this work has been made by Klebahn (Die Wirtsw. Rostpilze 397. 1904).

In America Arthur (Mycol. 4: 58. 1912), using aecial material on *Abies lasiocarpa* collected in Colorado, has succeeded in obtaining infection resulting in uredinia on *Cerastium oreophilum.*

21. Melampsoropsis Piperiana Arthur, N. Amer. Flora 7: 120. 1907.

On Ericaceae:

*Rhododendron Californicum* Hook.—Newport, Lincoln Co., June 2, 1892, A. Isabel Mulford (Specimen in Herb. N. Y. Bot. Gard. and in Herb. J. C. Arthur), May 16, 1914, G. H. Godfrey, *1280;* Larch Mt., Multnomah Co., Aug. 1910, *1118;* Parmelia Lake, near Mt. Jefferson, July 3, 1914, F. D. Bailey, *1939;* Trail to Hanging Valley, near Mt. Jefferson, Aug. 11, 1914, H. P. Barss & G. B. Posey, *1623.*

22. Melampsoropsis Pyrolae (DC.) Arth. Résult Sci. Congr. Bot. Vienne 338. 1906.

*Aecidium* (?) *Pirolae* DC. Fl. Fr. 6: 99. 1815.

*Aecidium conorum Piceae* Reess, Abh. Nat. Ges. Halle 11: 102. 1869.

*Chrysomyxa Pirolae* Rostr. Bot. Centr. 5: 127. 1881.

*Peridermium conorum Piceae* Arth. & Kern, Bull. Torrey Club 33: 431. 1906.

On Pinaceae: O, I.

*Picea Engelmanii* Parry—Sumpter, Baker Co., Sept. 25, 1909, G. G. Hedgcock, *1916*.

On Pyrolaceae: II, III.

*Pyrola secunda* L.—North slope Mt. Hood, Aug. 7, 1914, *1607;* Trail to Elk Meadows, Hood River Co., July 23, 1915, *3061;* Columbia Highway, Multnomah Co., Aug. 19, 1916, J. R. Weir, *269*.

*Pyrola* sp.—Grant's Pass, Josephine Co., Sept. 3, 1916, J. R Weir, *268*.

The genetic relation of this species with *Peridermium conorum Piceae* was first suggested by Rostrup (l. c.). So far as the writer is aware the first culture work confirming this observation was made by Fraser (Mycol. 4: 183. 1912), who succeeded in obtaining infection resulting in pycnia and aecia on the cones of *Picea mariana* and *P. canadensis*, following exposure to germinating telia on *Pyrola americana* and *P. elliptica*.

23. **Milesia Polystichii** Wineland n. sp.

O. and I. Unknown.

II. Uredinia hypophyllous, scattered, roundish, 0.2–0.3 mm. across, bullate, brownish yellow, tradily dehiscent by a central pore, peridium well developed, cells above polygonal, approximately isodiametric, diameter about 7 $\mu$, cells at the sides elongated to 21 $\mu$, outer walls 2–2.5 $\mu$, inner walls 2.5–3 $\mu$; urediniospores obovoid, ellipsoid, or oblong, 18–23 by 26–35 $\mu$, wall colorless, 1.5–2.5 $\mu$ in thickness, strongly and sparsely echinulate, pores obscure.

III. Telia unknown.

On Polypodiaceae:

*Polystichum munitum* (Kaulf.) Presl.—Grant's Pass, Josephine Co., Sept. 5, 1916, J. R. Weir, *260* (type).

This species was separated from material referred to *Hyalopsora laeviuscula* in the writer's herbarium by Miss Grace O. Wineland who has been studying the fern rusts of North America in this laboratory.

24. Pucciniastrum Abieti-Chamaenerii Kleb. Prings. Jahrb. f. Wiss. Bot. 34: 387. 1900.

On Pinaceae: I.

*Abies grandis* Lindl.—Dee, Hood River Co., July 23, 1915, *3355*.

*Abies lasiocarpa* Nutt.—North slope Mt. Hood, 4,500 ft., Aug. 9, 1914, *3295*.

On Onagraceae: II, III.

*Chamaenerion angustifolium* (L.) Scop.—Bonneville, Multnomah Co., Aug. 11, 1910, *1075;* Garden Home, Multnomah Co., Aug. 1911, *1990;* Southwest slope Mt. Jefferson, July 3, 1914, F. D. Bailey,

*3247;* Odell, Hood River Co., Aug. 5, 1914, *1618;* Crater Lake, Klamath Co., Sept. 21, 1913, E. P. Meinecke, *Cr Pk D (2) 2;* Portland, Aug. 24, 1915, E. Bartholomew (Barth., N. Am. Ured. *1482*).

This species is separated from *P. pustulatum* largely on the basis of culture investigations. All of the culture work has been conducted with the above host species or other members of the same genus or section of *Epilobium*. European investigators have amply demonstrated the connection of this form with aecia on *Abies* (Klebahn, Die Wirtsw. Rostpilze 393. 1904). In America, Fraser, working in Nova Scotia (Mycol. 4: 176. 1912), was the first to conduct culture experiments. He obtained, in three trials, the development of aecia on *Abies balsamea*, from sowings with teliosporic material from *C. angustifolium*. With the aecia thus obtained he sowed back to *Chamaenerion* and obtained uredinia. Weir & Hubert (Phytopath. 6: 373. 1916) conducted similar work with Idaho material and succeeded in obtaining the development of aecia on *Abies lasiocarpa*. The aecia thus obtained were sown back on the telial host (Phytopath. 7: 109. 1917), with the result that uredinia were developed in abundance.

25. Pucciniastrum Galii (Link) Fischer, Ured. d. Schweiz 471. 1904.

*Caeoma Galii* Link, in Willd. Sp. Pl. $6^2$: 21. 1825.

On Rubiaceae: II.

*Galium triflorum* Michx.—Corvallis, April 29, 1914, F. D. Bailey, *1992*, May 9, 1914, *1991*, July 5, 1914, H. P. Barss, *1996*, June 29, 1914, G. B. Posey, *1313*, July 10, 1915, *3104;* Oregon City, Clackamus Co., Aug. 20, 1915, E. Bartholomew, *5934* (Barth. N. Am. Ured. *1679*); Grant's Pass, Josephine Co., Sept. 3, 1916, J. R. Weir, *187*.

This species is known to the writer from North America only from the above collections and a specimen collected by J. W. Macoun in British Columbia in 1915, one from Palmer Lake, Colorado, Sept. 6, 1913, by E. Bethel, both in the Arthur Herbarium, and a collection made by Dr. H. Fitzpatrick and the writer at Michigan Hollow Swamp near Ithaca, N. Y., July, 1916. All are on *G. triflorum*. The species is evidently common in western Oregon and if aecia are developed, doubtless occur on *Abies grandis*. Field observations made by the writer, however, would indicate that this rust winters over in the uredinial stage.

26. Pucciniastrum Goodyerae (Tranz.) Arth. N. Am. Fl. 7: 105. 1907.

*Uredo Goodyerae* Tranz. Trudi S. Peterb. Obshch. Est. Otd. Bot. 23: 28. 1893.

On Orchidaceae: II.

*Goodyera Menziesii* (Lindl.) Morong.—Parmelia Lake, West slope Mt. Jefferson, July 3, 1914, F. D. Bailey, *1627;* North slope Mt. Hood, Aug. 9, 1914, *1620.*

27. Pucciniastrum Myrtilli (Schum.) Arth. Résult. Sci. Congr. Bot. Vienne 337. 1906.

*Aecidium ? Myrtilli* Schum. Enum. Pl. Saell. **2**: 227. 1803.

*Pucciniastrum Vacciniorum* (DC.) Dietel, in E. & P. Nat. Pfl. $1^{1**}$: 47. 1897.

On Vacciniaceae: II.

*Oxycoccus macrocarpus* (Ait.) Pursh—Astoria, Clatsop Co., Aug. 1916, G. M. Darrow, comm. C. L. Shear *2905.*

*Vaccinium caespitosum* Michx.—Mary's Peak, Benton Co., Aug. 15, 1914, *1517, 1520.*

*Vaccinium macrophyllum* (Hook.) Piper—Whitewater Ranger Station, West slope Mt. Jefferson, Aug. 12, 1914, H. P. Barss & G. B. Posey, *3314;* Ashland, Jackson Co., Sept. 10, 1914, *3316.*

*Vaccinium ovatifolium* Sm.—Whitewater Ranger Station, West slope Mt. Jefferson, Aug. 12, 1914, H. P. Barss & G. B. Posey, *3315.*

*Vaccinium* sp.—North slope Mt. Hood, 4,000 ft., Aug. 7, 1914, *1606, 1609;* Sucker Creek, Josephine Co., July 27, 1913, E. P. Meinecke, *Si (D6) D3.*

Clinton (Rep. Conn. Agr. Exp. Sta. **1909–1910**: 719. 1911) was the first to show that the aecial stage of this species occurred on *Tsuga canadensis.* He successfully infected *Gaylussacia baccata* by sowing with aeciospores from *Tsuga,* resulting in the development of the typical uredinia of this species.

Fraser in 1912 (Mycol. **5**: 237. 1913) confirmed Clinton's work by obtaining the development of aecia on the leaves of *Tsuga canadensis* following sowings from teliosporic material on *Vaccinium canadense.* The same author in 1913 (Mycol. **6**: 27. 1914) obtained aecia on *Tsuga canadensis* following sowing of teliosporic material from *Gaylussacia resinosa.* The aecia developed in these experiments are similar to those of *Peridermium Peckii,* but may represent an undescribed form.

No aecia collected in the west have been referred to this species though they doubtless occur on *Abies* or *Tsuga heterophylla.*

28. Pucciniastrum pustulatum (Pers.) Dietel, in E. & P. Nat. Pfl. $1^{1**}$: 47. 1897.

*Uredo pustulata* Pers. Syn. Fung. 219. 1801.

On Onagraceae:

*Epilobium adenocaulon* Haussk.—Corvallis, Oct. 29, 1911, F. D.

Bailey, *1173*, Nov. 4, 1911, F. D. Bailey, *1171*, June 18, 1914, F. D. Bailey, *3218*, July 29, 1914, *1480;* Hilgard, Union Co., July 10, 1914, *1533*, *1535*, Glendale, Douglass Co., July 17, 1914, *1505*, North slope Mt. Hood, Aug. 7, 1914, *1488;* Whitewater Ranger Station, West slope Mt. Jefferson, H. P. Barss & G. B. Posey, *3219;* Ashland, Jackson Co., Sept. 10, 1914, *3221*.

*Epilobium brevistylum* Barbey—Corvallis, July 14, 1914, G. B. Posey, *3220*.

No successful culture work has been conducted with this form, as here interpreted, either in Europe or America. Aecia doubtless occur on species of *Abies*.

From field observations it is quite evident that in western Oregon at least this species overwinters in the uredinial stage.

29. Pucciniastrum Pyrolae (Pers.) Dietel, in E. & P. Nat. Pfl. $1^{1**}$: 47. 1897.

*Aecidium Pyrolae* Pers. Gmel. Syst. Nat. 2: 1473. 1791.

*Uredo Chimaphilae* Peck, Ann. Rep. N. Y. State Mus. 46: 33. 1893.

On Pyrolaceae:

*Chimaphila umbellata* (L.) Nutt. (*C. occidentalis* Rydb.)—Spencer Creek, Klamath Co., 5,000 ft., July 10, 1903, E. B. Copeland, *3714* (Sydow, Ured. *1795*); Whitewater Creek along trail to Hanging Valley, Mt. Jefferson, Aug. 11, 1914, H. P. Barss & G. B. Posey, *1908;* North slope Mt. Hood, Aug. 7, 1914, *1614*.

*Pyrola secunda* L., Klamath Co., July 10, 1903, E. B. Copeland (Sydow, Ured. *1791*).

30. Pucciniastrum sparsum (Wint.) E. Fischer, Beitr. Krypt. Schweiz $2^2$: 469. 1904.

*Melampsora sparsa* Wint. in Rab. Krypt. Fl. $1^1$: 245. 1881.

On Ericaceae:

*Arbutus Menziesii* Pursh—Myrtle Creek, Douglass Co., June 8, 1914, F. D. Bailey, *1837;* Glendale, Douglass Co., July 17, 1914, *1298;* Ashland, Jackson Co., Sept. 10, 1914, *1838;* Corvallis, April, 1911, *3374;* Grant's Pass, Josephine Co., Sept. 3, 1916, J. R. Weir, *244*.

*Arctostaphylos Manzanita* Parry—Grant's Pass, Josephine Co., Sept. 3, 1916, J. R. Weir, *245*, *247*.

*Arctostaphylos nevadensis* A. Gray—Northwest slope Mt. Jefferson, Aug. 14, 1914, H. P. Barss & G. B. Posey, *3290*.

No aecial collections have been referred to this species in America. Fischer (Cent. für Bakt. 46: 333. 1916) has cultured this species. He used germinating telial material on *Arctostaphylos alpina* and sowed

on species of *Abies* and *Picea*, obtaining the development of pycnia and aecia on *Picea excelsa*. This is the only case in which culture investigations have shown the aecia of *Pucciniastrum* to occur on *Picea*.

31. Uredinopsis Copelandii Sydow, Ann. Myc. **2**: 34. Feb. 1904.
*Uredinopsis Atkinsonii* Magn. Hedwigia **43**: 123. Mar. 1904.
*Peridermium balsameum* Peck, Rept. N. Y. State Mus. **27**: 104. 1875. p.p.

On Pinaceae: I.

*Abies grandis* Lindl.—Trail to Sulphur Springs, Corvallis, Benton Co., Nov. 7, 1914, *3339;* Corvallis, Feb. 2, 1914, *3300.*

*Abies nobilis* Lindl.—Mary's Peak, Benton Co., Feb. 7, 1914, F. D. Bailey, *3337,* Aug. 15, 1914, *3334, 3335, 3336, 3338.*

On Polypodiaceae: II, III.

*Athyrium cyclosorum* Rupr.—Hoover, Linn Co., Aug. 19, 1914, H. P. Barss & G. B. Posey, *3032;* Mary's Peak, Benton Co., Aug. 15, 1914, *3033, 3034;* Elk City, Lincoln Co., Aug. 20, 1914, *2675;* Hood River Co., July 23, 1915, *3031;* Grant's Pass, Josephine Co., Sept. 5, 1916, J. R. Weir, *258;* Yaquina, Lincoln Co., July 17, 1915, *3035.*

There seems to be no good reason for separating *U. Copelandii* Sydow from *U. Atkinsonii.* All gradations in the length of the beak of the urediniospores are found on the above collections. Most of the material has urediniospores with long beaks and some of the collections show spores with both long and short beaks.

Field observations as well as a study of morphological characters would support the view that the aecia commonly referred to *Peridermium balsameum* occurring on *Abies grandis* and *A. nobilis* in western Oregon are genetically connected.

Fraser (Mycol. **5**: 236. 1913) has cultured *U. Atkinsonii* by sowing aeciospores of *Peridermium balsameum* on *Aspidium Thelepteris* followed sparingly by the development of uredinia.

32. Uredinopsis Pteridis Dietel & Holway, Ber. Deuts. Bot. Ges. **13**: 331. 1895.
*Aecidium pseudo-balsameum* Diet. & Holw. Erythea **7**: 98. 1899.
*Peridermium pseudo-balsameum* Arth. & Kern, Bull. Torrey Club **33**: 430. 1906.

On Pinaceae: I.

*Abies amabilis* (Loud.) Forb.—Whitewater Creek, near Mt. Jefferson, Aug. 11, 1914, H. P. Barss & G. B. Posey, *3294.*

*Abies grandis* Lindl.—Corvallis, Aug. 1910, *3299,* May 8, 1909, comm. Clarence D. Learn, April 29, 1914, F. D. Bailey, *3303;* Ump-

qua Nat. Forest, near Diston, Lane Co., Oct. 27, 1909, Geo. G. Hedgcock; Philomath, Jan. 6, 1914, *3298;* Wren, Benton Co., Aug. 3, 1914, *3296;* Ashland, Jackson Co., Sept. 10, 1914, *3297;* Mary's Peak, Benton Co., Feb. 7, 1914, G. H. Godfrey, *3301*, Aug. 15, 1914, *3302;* N. slope Mt. Hood, 4,000 ft., Aug. 9, 1914, *1616.*

On Polypodiaceae: II, III.

*Pteridium aquilinum pubescens* Underw.—Corvallis, Sept. 1909, *1142*, July, 1910, *1082*, Aug. 1910, *1058*, Oct. 6, 1914, *3109;* Bonneville, Multnomah Co., Aug. 11, 1910, *1076;* Scappose, Columbia Co., July 25, 1911, *1067;* North slope Mt. Hood, Aug. 9, 1914, *1617;* Ashland, Jackson Co., Sept. 10, 1914, *1993;* Portland, Aug. 24, 1915, E. Bartholomew (Barth. N. Am. Ured. *1485*); Grant's Pass, Josephine Co., Sept. 5, 1916, J. R. Weir, *259.*

This species in all its stages is very common in western Oregon and the association of the infected aecial and telial hosts is everywhere apparent.

From field observations made by the writer and others it has been assumed that *Peridermium pseudo-balsameum* was the aecial stage of this species. Recently Weir and Hubert (Am. Jour. Bot. 4: 328–332. 1917) have conducted cultures showing the genetic connection of this species with aecia on *Abies grandis.* The authors evidently do not consider the aecia identical with *P. pseudo-balsameum.* The description which they give, however, agrees very well with the type of that species.

According to the writer's present interpretation, there are two closely related species of *Peridermium* on *Abies grandis* in western Oregon. One is to be referred to *P. balsameum* and is presumably genetically connected with *Uredinopsis Copelandii* (cf. 31). The other is *P. pseudo-balsameum* and is genetically connected with the species under discussion.

The walls of the aeciospores in *P. balsameum* are considerably thinner than those of *P. pseudo-balsameum.* In the former they are 1–1.5 $\mu$ while in the latter they are 2–2.5 $\mu$ in thickness.

## PUCCINIACEAE

33. Earlea speciosa (Fr.) Arth. Résult Sci. Congr. Bot. Vienne 341. 1906.

*Aregma speciosa* Fr. Syst. Myc. 3: 496. 1832.

*Phragmidium speciosum* Cooke, Grevillea 3: 171. 1875.

On Rosaceae:

*Rosa gymnocarpa* Nutt.?—I, Austin, Grant Co., Aug. 1915, J. R. Weir, *188.*

34. Gymnosporangium Betheli Kern, Bull. Torrey Club 34: 459. 1907.

*Roestelia Betheli* Kern, Bull. Torrey Club 34: 461. 1907.

On Malaceae: I.

*Crataegus Douglasii* Lindl.—Joseph, Wallowa Co., Aug. 19, 1899, C. L. Shear (Ellis & Ev. Fungi Columb. *1480*).

On Juniperaceae: III.

*Juniperus occidentalis* Hook.—Whitney, Baker Co., Aug. 1915, J. R. Weir, *170*.

Another specimen on *Crataegus* sp. indet. from eastern Oregon (ex herb. Ellis) bearing no date is in the Arthur herbarium and has been examined by the writer.

The life history of this species was first demonstrated by Arthur (Jour. Myc. 14: 23. 1908) and later repeatedly confirmed. Telia are otherwise known only on *Juniperus scopulorum* from Colorado, Idaho and Montana. Aecia are known to occur only on *Crataegus* sp. in the Rocky Mt. region and in eastern Oregon and Washington.

35. Gymnosporangium Blasdaleanum (Dietel & Holway) Kern, Bull. N. Y. Bot. Gard. 7: 437. 1911.

*Aecidium Blasdaleanum* Dietel & Holway, Erythea 3: 77. 1895.

*Gymnosporangium Libocedri* Kern, Bull. Torrey Club 35: 509. 1908.

On Malaceae: I.

*Amelanchier florida* Lindl.—Eugene, Lane Co., July 11, 1914, G. B. Posey, *3276;* Albany, Linn Co., June 11, 1913, D. W. Rumbaugh, *3171;* Cottage Grove, Lane Co., June 13, 1913, *3168*, June 20, 1913, C. E. Stewart, *3177;* Lebanon, Linn Co., Aug. 2, 1913, F. D. Bailey, *3174;* Crater Lake, Klamath Co., 7,000 ft., Sept. 4, 1913, E. P. Meinecke, *Cr Pk D 11;* Jackson Co., July, 1914, F. C. Reimer, *1791;* Between Albany and Lebanon, Linn Co., June 13, 1913, C. E. Roberts, *1788;* Lost Prairie, Sept. 1891, M. Craig; Halsey, Linn Co., June 9, 1913, *3170;* Corvallis, July 29, 1915, *3150;* Ashland, Jackson Co., Sept. 10, 1914, *3047;* N. W. Mt. Jefferson, Whitewater station, Aug. 17, 1914, H. P. Barss & G. B. Posey, *3043*, Aug. 28, 1916, H. P. Barss.

*Crataegus Douglasii* Lindl.—Halsey, Linn Co., June 9, 1913, *3214;* Albany, Linn Co., D. W. Brumbaugh, *3212;* Cottage Grove, Lane Co., May 21, 1913, *3169*, June 14, 1913, *3209;* Eugene, Lane Co., May 8, 1913, *3173*.

*Cydonia japonica* Pers.—Eugene, Lane Co., June, 1914, G. H. Godfrey.

*Cydonia vulgaris* L., Halsey—Linn Co., June 9, 1913, *3166;* Irving, Lane Co., 1913, Comm. S. J. Quigley, *1871;* Creswell, Lane Co.,

May 5, 1913, Comm. K. V. Miller, *1873;* Eugene, Lane Co., Aug. 1912, *1084;* Talent, Jackson Co., May 18, 1916, F. C. Reimer.

*Pyrus baccata* Linn.—Lorane Valley, Lane Co., May, 1915, C. E. Stewart, *3387.*

*Pyrus communis* L.—Kerby, Josephine Co., June 1, 1899, Comm. E. F. Meissner, *1845;* Brownsville, Linn Co., May 24, 1913, D. W. Brumbaugh, *1911;* Eugene, Lane Co., May 8, 1913, *3172,* April 22, 1915, *2620.*

*Pyrus diversifolia* Bong. (*P. rivularis* Dougl.)—Cottage Grove, Lane Co., June 13, 1913, *3175, 3211.*

*Pyrus ioensis* (Wood) Bailey—Cottage Grove, Lane Co., June 13, 1913, *1854;* Eugene, Lane Co., May 21, 1913, *3210.*

*Pyrus malus* L.—Eugene, Lane Co., July 10, 1913, J. O. Holt, *1787;* Cottage Grove, Lane Co., May 23, 1913, C. E. Stewart, *1913,* June 20, 1915, C. E. Stewart, *887.*

*Sorbus aucuparia* Linn.—Cottage Grove, Lane Co., June 13, 1913, *3178;* Eugene, Lane Co., June 1, 1914, G. H. Godfrey, *3222.*

*Sorbus hybrida* Linn.—Cottage Grove, Lane Co., May 21, 1913, *3176,* June 13, 1913, *3167.*

On Juniperaceae:

*Libocedrus decurrens* Torr.—Eugene, Lane Co., Feb. 28, 1913, *3213,* Feb. 21, 1914, F. D. Bailey, *1675,* Mar. 20, 1914, *3070;* Breitenbush Hot Springs, Marion Co., Mar. 27, 1915, E. A. Hartley, *2621;* Cottage Grove, Lane Co., Mar. 8, 1914, C. E. Stewart, *1888;* Ashland, Jackson Co., Sept. 10, 1914, *1839;* Corvallis, Mar. 30, 1915, J. G. Corsaut, *901;* Grant's Pass, Josephine Co., Sept. 3, 1916, J. R. Weir, *185.*

This species is very common in its aecial stage on all the native members of the Malaceae as well as most of the cultivated fruits and ornamental plants belonging to this family which may occur in the range of the incense cedar. There is considerable evidence also that the disease is gradually spreading beyond the natural range of the telial host. Observations made at Corvallis support this view. Previous to 1915 no specimens of this species had been collected in Benton County though careful search had been made many times. The incense cedar does not occur naturally in that locality but is frequently planted for ornament. There are several fine examples on the campus at the Oregon Agr. College. In 1915 a very sparing infection of the aecial stage was found in the vicinity on native hosts only, and the cedar trees on the campus were found to be sparingly infected. Reports of the occurrence on quince have come from Salem, far north of the natural range of the incense cedar. The writer believes that the disease will gradually spread throughout the Wil-

lamette Valley on the incense cedars planted for ornament and, in certain cases, will become a serious menace to cultivated pears and quinces.

The life history of the species was first worked out by Arthur (Mycol. 1: 252. 1909; 4: 57. 1912). He succeeded in showing that aecia occurred on *Crataegus* and *Amelanchier*. The telial material used for the cultures was collected at Eugene, Oregon, by Prof. A. R. Sweetzer. The writer has also studied this species in some detail (Phytopath. 4: 261–269. 1914; Ore. Expt. Sta. Biennial Crop Pest Rep. II: 204–212. 1915) and has reported the results of culture work and field observations. Similar work is also briefly reported by O'Gara (Science N. S. 39: 620–621. 1914). The previous records of the occurrence of this species on *Malus floribundus* Siebold and *Sorbus sambucifolia* Roem. made by the writer (l. c.) should be corrected to read *Pyrus ioensis* and *S. aucuparia* respectively. For the correct determination of these hosts the writer is indebted to Prof. W. W. Eggleston.

This species has since been successfully cultured in the greenhouse on *Pyrus sinensis* by Prof. H. P. Barss. The writer, using aecial material on quince, the result of infection experiments made in 1914, has obtained sparing infection on *Libocedrus* resulting in telia which matured in February 1915. The trees were kept in the greenhouse at the Oregon Agr. College.

36. Gymnosporangium Harknessianum (Ell. & Ev.) Kern, Bull. N. Y. Bot. Gard. 7: 441. 1911.

*Roestelia Harknessiana* Ell. & Ev. Kern, Bull. Torrey Club 34: 462. 1907.

On Malaceae: I.

*Amelanchier alnifolia* Nutt.—Redmond, Crook Co., July 2, 1914, *1393;* Fort Rock, Lake Co., Oct. 10, 1915, Wendover, *3375*.

This very interesting species has otherwise been reported only from northern California. The telia form is unknown. In the collection made by the writer listed above, the aecia occurred only on fruits and twigs. There was every evidence that this fungus is perennial. Some of the specimens show fresh aecia on branches having four annual rings, surrounding or extending from cankered areas bearing evidence of old aecial cups. There is slight hypertrophy. The branches are frequently girdled and killed.

37. Gymnosporangium juniperinum (L.) Mart. Fl. Crypt. Erlang. 333. 1817.

*Tremella juniperina* L. Sp. Pl. 1157. 1753.

On Malaceae: I.

*Sorbus occidentalis* (S. Wats.) Greene—North slope Mt. Jefferson, along trail to Hanging Valley, Aug. 15, 1914, H. P. Barss & G. B. Posey, *1395;* Columbia Highway, Multnomah Co., Aug. 19, 1916, J. R. Weir, *279.*

On Juniperaceae: III.

*Juniperus sibirica* Burg.—North slope Mt. Jefferson, Aug. 26, 1916, H. P. Barss, *3399.*

The genetic connection of the forms of this alpine species has been abundantly demonstrated by European investigators, first by Hartig (Lerb. Baum-Kr. 133. 1882), and later by many others. Arthur in 1911 (Mycol. 4: 57. 1912), using telial material from *J. sibirica* collected in Colorado, succeeded in obtaining infection resulting in pycnia only on *Sorbus americana.* The species is known in America only from the Rocky and Cascade Mountains of the United States and Canada.

38. Gymnosporangium juvenescens Kern, Bull. N. Y. Bot. Gard. 7: 448. 1911.

On Malaceae: I.

*Amelanchier* sp.—Hurricane Creek, Wallowa Co., July 24, 1897, E. P. Sheldon, *8622.*

On Juniperaceae: III.

*Juniperus scopulorum* Sarg.—White Pine, Baker Co., Aug. 1915, J. R. Weir, *169.*

This species causes witches' brooms on the telial host somewhat similar to the eastern *G. nidus-avis* Thax.

Arthur has repeatedly cultured it, showing that the aecia occur on *Amelanchier* and *Sorbus* (Jour. Myc. 13: 203. 1907; 14: 18. 1908; Mycol. 1: 239. 1909; 4: 195. 1912).

39. Gymnosporangium Kernianum Bethel, Mycologia 3: 157. 1911.

On Juniperaceae: III.

*Juniperus occidentalis* Hook.—Redmond, Crook Co., July 2, 1914, *1392,* May 15, 1915, *3390.*

The above specimens are somewhat doubtfully referred to this species. The witches' brooms are large and open, sometimes reaching 2–3 feet in diameter. The teliospores are somewhat more tapering at the apex than is typical for the species and average shorter and somewhat narrower, 19–22 by 45–65 $\mu$. The only aecia collected in the vicinity are properly referred to *G. Harknessianum.* There was no very direct field evidence, and unless the above collections represent an undescribed form there is little possibility that the two can be genetically connected. Arthur (Mycol. 4: 62. 1912) has cultured

*G. Kernianum* on *Amelanchier* but obtained the development of pycnia only. Field observations and collections by Bethel in Colorado indicate strongly that the aecial stage occurs on *Amelanchier*. The *Roestelia*, however, is quite different from *R. Harknessiana*.

40. Gymnosporangium koreaense (P. Henn.) Jackson, Jour. Agr. Research 5: 1006. 1916.

*Roestelia koreaensis* P. Henn. in Warburg, Monsunia 1: 5. 1899.

*Gymnosporangium asiaticum* Miyabe, Bot. Mag. Tokyo 17: 34. 1903. (Hyponym.)

*Gymnosporangium Haraeanum* Syd. Ann. Myc. 10: 405. 1912.

*Gymnosporangium chinense* Long, Jour. Agr. Research 1: 353. 1914.

On Malaceae: I.

*Pyrus sinensis* Lindl.—Portland (Orient), June 11, 1914, *2666*.

On Juniperaceae: III.

*Juniperus chinensis* L.—Portland (Orient), March 29, 1915, *2668*.

This species has been shown by the writer (l. c.) to have been established at Portland (Orient), Oregon, on trees imported from Japan. It has been cultured on *Pyrus sinensis* and *Cydonia vulgaris*.

41. Gymnosporangium Nelsoni Arth. Bull. Torrey Club 28: 665. 1901.

On Juniperaceae: III.

*Juniperus occidentalis* Nutt.—Austin, Grant Co., April, 1916, J. R. Weir, *257*.

*Juniperus scopulorum* Sarg.—Whitman Nat. Forest, Aug. 1915, J. R. Weir, *166*.

This species causes conspicuous galls on the branches of *Juniperus*. The aecial stage has been collected on *Amelanchier*, *Cydonia*, *Peraphyllum*, *Pyrus* and *Sorbus*.

Arthur (Mycol. 4: 61. 1912; 7: 78. 1915) has conducted cultures, using telial material from Colorado. Weir & Hubert (Phytopath. 7: 109. 1917) have recently confirmed these results, using material collected in Montana, on *J. communis* and *J. scopulorum*.

42. Gymnosporangium nootkatensis (Trel.) Arth. Am. Jour. Bot. 3: 44. 1916.

*Uredo nootkatensis* Trelease, Alaska Harr. Exped. 5: 36. 1904.

*Uredo Chamaecyparidis-nutkaensis* Tubeuf, Nat. Zeits. Forst.-Landw. 2: 91. 1914.

On Juniperaceae:

*Chamaecyparis nootkatensis* (Lamb.) Spach—North slope Mt. Jefferson, trail to Hanging Valley, Aug. 15, 1914, H. P. Barss & G. B.

Posey, *1394;* Whitewater Ranger station, Aug. 28, 1916, H. P. Barss; Foot of Mt. Jefferson, Aug. 28, 1916, H. P. Barss.

The material collected by Barss and Posey in 1914 contained teliospores in the uredinia and forms the basis of the transfer of the very interesting and much discussed *Uredo nootkatensis* to *Gymnosporangium.* A full account of the history of this species has been given by Arthur (l. c.). In the collections of 1916 made in the same locality by Prof. Barss, teliospores were found in great abundance with the uredinia, and in many sori predominated. The urediniospores were germinated in this laboratory and the germ tubes found to develop in the usual way for urediniospores.

43. Gymnosporangium Sorbi (Arth.) Kern, Bull. N. Y. Bot. Gard. 7: 438. 1911.

*Aecidium Sorbi* Arth. Bull. Torrey Club 33: 521. 1906.

On Malaceae: I.

*Sorbus occidentalis* (S. Wats.) Greene—Whitewater Ranger station, Mt. Jefferson, Aug. 28, 1916, H. P. Barss.

There is little doubt that the suggestion of the genetic relationship of this species with *Gymnosporangium nootkatensis* (cf. 42) originally made by Kern (Science 31: 833. 1910) and later re-affirmed by Arthur (Am. Jour. Bot. 3: 43–44. 1916) will prove to be correct. The above collection extends the range of the aecia to correspond exactly with the range of the known collections of uredinia and is the most southern record.

It seems best, however, for the purpose of this list to retain the above name till actual cultures confirming the prediction have been made.

44. Gymnosporangium tubulatum Kern, Bull. N. Y. Bot. Gard. 7: 451. 1911.

*Roestelia tubulata* Kern; in M. E. Jones, Bull. Univ. Mont. 61: 64. 1910.

On Malaceae: I.

*Crataegus Douglasii* Lindl.—Minam River, Wallowa Co., Oct. 5, 1897, E. P. Sheldon, *9061;* Wallowa Nat. Forest, Sept. 28, 1910, G. G. Hedgcock, *1944.*

The above collections were found in the Arthur herbarium at the Purdue University Experiment Station. The specimens show chiefly foliage infection, though the first-mentioned collection also includes infected fruit.

Weir (Phytopath. 5: 218. 1915) has recently demonstrated by cultures that the telia, which were previously unknown, occur on the twigs of *Juniperus scopulorum* forming irregularly lobed galls. Telia

have been collected only in Idaho and western Montana. Weir and Hubert in 1916 (Phytopath. 7: 109. 1917) have confirmed the above results.

45. KUNKELIA NITENS (Schw.) Arth. Bot. Gaz. 63: 504. 1917.
*Aecidium nitens* Schw. Schrift. Nat. Ges. Leipzig 1: 69. 1822.
ON ROSACEAE:
*Rubus nigrobaccus* Bailey—Freewater, Umatilla Co., June 27, 1913, F. D. Bailey, *1143*.
*Rubus vitifolius* Cham. & Schlecht. (cult. loganberry)—LaGrand, Union Co., July 20, 1914, C. C. Cate, *1851*.
Kunkel's results (Bull. Torrey Club 40: 361. 1913; 43: 559. 1916; Amer. Jour. Bot. 1: 37. 1914) indicate that two rusts on *Rubus*, both commonly referred to *Gymnoconia interstitialis* or *Caeoma nitens*, occur in North America, one a short-cycled form having the morphology of a *Caeoma*, the other a brachy-form with caeomoid aecia and telia of the type of *Puccinia* (*P. Peckiana* Howe). Arthur (l. c.) has recently based the genus *Kunkelia* on the short-cycled form.
The inclusion of the Oregon collections under *Kunkelia* follows the disposition made of them by Arthur.

46. NYSSOPSORA ECHINATA (Lev.) Arth. Result. Sci. Congr. Bot. Vienne 342. 1906.
*Triphragmium echinatum* Lev. Ann. Sci. Nat. III. 9: 247. 1848.
ON UMBELLIFERAE:
*Ligusticum Cusickii* Coult. & Rose—Steins Mts., Harney Co., Aug. 1901, Griffiths & Morris (Griffiths, W. Am. Fungi *340*).
*Ligusticum purpureum* Coult. & Rose—North slope Mt. Jefferson, Aug. 13, 1914, H. P. Barss & G. B. Posey, *2540*.

47. PHRAGMIDIUM DISCIFLORUM (Tode) J. F. James, Contr. U. S. Nat. Herb. 3: 276. 1895.
*Ascophora disciflora* Tode, Fungi Meckl. 1: 16. 1790.
ON ROSACEAE:
*Rosa* sp. cult.—Empire, Coos Co., Oct. 2, 1911, comm. J. R. Brown, *3154;* Portland, May 10, 1914, comm. W. C. Dietz, *3156;* Eugene, Lane Co., June 1, 1914, G. H. Godfrey, *3147*; Sutherlin, Douglass Co., March 9, 1915, comm. Gladys Franz, *2511*.

48. PHRAGMIDIUM IMITANS Arth. N. Am. Flora 7: 165. 1912.
ON ROSACEAE:
*Rubus leucodermis* Dougl., Philomath, May 10, 1914, *1830*.
*Rubus neglectus* Pk., Ore. Agr. Coll. Pathologium, Corvallis, July 30, 1915, *3027*.
*Rubus strigosus* Michx.—Stream banks, Eastern Oregon, 4,000–5,000 ft. elev., July, 1897, W. C. Cusick, *1729*.

49. PHRAGMIDIUM IVESIAE Sydow, Ann. Myc. 1: 329. 1903.
*Phragmidium affine* Sydow, Ann. Myc. 2: 29. 1904.
ON ROSACEAE:
*Potentilla blaschkeana* Turcz.—Philomath, June 20, 1910, *1503;* Austin, Grant Co., June, 1913, J. R. Weir, *147;* Baker Co., June, 1913, J. R. Weir, *17;* Sumpter, Baker Co., June, 1913, J. R. Weir, *3;* Hilgard, Union Co., July 10, 1914, *1534.*
*Potentilla glomerata* A. Nels.—Andrews, Harney Co., Aug. 1901, Griffiths & Morris (Griffiths, West Am. Fungi *511b*).
*Potentilla gracilis* Dougl.—Corvallis, June 20, 1909, E. R. Lake, *1499,* July 29, 1914, *1477;* Wren, Benton Co., June 26, 1914, *1323.*
*Potentilla* sp.—Corvallis, June, 1910, *1110, 3149,* Aug. 1911, F. D. Bailey, *1071.*

50. PHRAGMIDIUM JONESII Dietel, Hedwigia 44: 128. 1905.
ON ROSACEAE:
*Ivesia Baileyi* S. Wats.—Steins Mts., Harney Co., July 27, 1898, W. C. Cusick, Phan. Herb. *1967.* (From specimen in herb. Field Museum *108727.*)

51. PHRAGMIDIUM MONTIVAGUM Arth. Torreya 9: 24. 1909.
ON ROSACEAE:
*Rosa gymnocarpa* Nutt.—North slope Mt. Hood, Aug. 9, 1914, *1478;* Bank of Minam River, Union Co., alt. 5,100 ft., Oct. 4, 1897, E. P. Sheldon, *9053.*
*Rosa pisocarpa* Gray?—Hilgard, Union Co., July 10, 1914, *1537.*
*Rosa* sp.—Trail Creek Cañon, Wallowa Co., May 18, 1897, E. P. Sheldon, *8073;* Corvallis, May 1, 1914, *1466,* April 25, 1915, G. B. Posey & C. M. Schearer, *3153,* April 28, 1915, *3151;* North slope Mt. Hood, Aug. 7, 1914, *1619;* Mouth of Salmonberry River, Tillamook Co., July 17, 1915, G. VanGundia, *3089.*

52. PHRAGMIDIUM OCCIDENTALE Arth.; Earle, in Greene, Pl. Baker. 2: 3. 1901.
ON ROSACEAE:
*Rubus parviflorus* Nutt.—Wallowa Lake, Wallowa Co., Aug. 1899, C. L. Shear, *952* (Griffiths, W. Am. Fungi *329*); Jackson Co., July 9, 1903, E. B. Copeland (Sydow, Ured. *1788*); Mt. Hood, Aug. 31, 1901, E. W. D. Holway, Aug. 7, 1914, *1636;* Glen Brook, Benton Co., Aug. 1909, *1119;* Trail to Hanging Valley, Mt. Jefferson, H. P. Barss & G. B. Posey, *1785;* Mary's Peak, Benton Co., Aug. 15, 1914, *1285;* Elk City, Lincoln Co., Aug. 20, 1914, *1626;* Dothan, Douglass Co., Sept. 8, 1914, *1930;* Corvallis, May 4, 1915, *3059;* Unity, Baker Co., Aug. 1915, J. R. Weir, *242;* Austin, Grant Co., Aug. 1916, J. R. Weir, *238.*

53. PHRAGMIDIUM POTENTILLAE (Pers.) P. Karst. Bidr. Finl. Nat. Folk 31: 49. 1879.

*Puccinia Potentillae* Pers. Syn. Fung. 229. 1801.

ON ROSACEAE:

*Potentilla aracnoides* Lehm.—Austin, Grant Co., Aug. 1915, J. R. Weir, *161*.

*Potentilla Hippiana* Lehm.—Austin, Grant Co., Aug. 1915, J. R. Weir, *158*.

54. PHRAGMIDIUM ROSAE-ACICULARIS Liro, Bidr. Finl. Nat. Folk. 65: 428. 1908.

ON ROSACEAE:

*Rosa nutkana* Presl.—Bridal Veil, Multnomah Co., May 18, 1915, *3348;* Edge of woods on Minam River, Union Co., Aug. 11, 1897, E. P. Sheldon, *8667*.

*Rosa* sp.—Corvallis, July 28, 1914, *3146*.

55. PHRAGMIDIUM ROSAE-CALIFORNICAE Dietel, Hedwigia 44: 125. 1905.

ON ROSACEAE:

*Rosa gymnocarpa* Nutt.—Corvallis, July 29, 1914, H. P. Barss, *1469;* Mary's Peak, Benton Co., Aug. 15, 1914, *1512, 1519, 1521;* Ashland, Jackson Co., Sept. 10, 1914, *3084*.

*Rosa nutkana* Presl.—Corvallis, July 29, 1914, *1473;* Portland, Aug. 23, 1915, E. Bartholomew, *5950* (Barth. N. Amer. Ured. *1626*); Hood River, Aug. 26, 1915, E. Bartholomew, *5973* (Barth. Fungi Columb. *4834*); Austin, Grant Co., Aug. 1915, J. R. Weir, *157;* Bend, Crook Co., Sept. 11, 1916, J. R. Weir, *202*.

*Rosa pisocarpa* Gray—Corvallis, April 5, 1914, *1523*.

*Rosa* sp.—Bonneville, Multnomah Co., Aug. 11, 1910, *1072,* Corvallis, Aug. 10, 1911, *3152*, Spring 1914, H. C. Gilbert, *3155,* Eugene, Lane Co., July 11, 1914, G. B. Posey, *1467;* Ashland, Jackson Co., Sept. 30, 1914, *3350;* Whitewater Creek, near Mt. Jefferson, Aug. 11, 1914, H. P. Barss & G. B. Posey, *3362*.

56. PILEOLARIA TOXICODENDRI (Berk. & Rav.) Arth. N. Am. Flora 7; 147. 1907.

*Uromyces Toxicodendri* Berk. & Rav. Grevillea 3: 56. 1874.

*Pileolaria brevipes* Berk. & Rav. Grevillea 3: 58. 1874.

ON ANACARDIACEAE:

*Rhus diversiloba* T. & G.—Corvallis, April 29, 1914, F. D. Bailey, *1831;* Grant's Pass, Josephine Co., Sept. 5, 1916, J. R. Weir, *256;* Jim Creek, Wallowa Co., June 14, 1897, E. P. Sheldon, *8279*.

57. POLYTHELIS FUSCA (Pers.) Arth. Résult. Sci. Cong. Bot. Vienne 341. 1906.

*Aecidium fuscum* Pers., in Gmel. Syst. Nat. 2: 1473. 1791.

On Ranunculaceae:

*Anemone oregana* A. Gray—Mary's Peak, Benton Co., May 23, 1915, *3030*.

*Anemone quinquefolia* L.?—North slope Mt. Hood, Aug. 9, 1914, *1621*.

58. Puccinia Absinthii (Hedw. f.) DC. Fl. Fr. **6**: 56. 1815.

*Uredo* (*Puccinia*) *Artemisii* Hedw. f.; DC. in Lam. Encycl. Meth. Bot. **8**: 245. 1808.

*Puccinia similis* E. & E. Bull. Torrey Club **25**: 508. 1898.

On Carduaceae:

*Artemisia dracunculoides* Pursh—Sherman, Sherman Co., July 1, 1914, *2671*, May 16, 1915, *2672*.

*Artemisia frigida* Willd.—Bend, Crook Co., Sept. 11, 1916, J. R. Weir, *212*.

*Artemisia ludoviciana* Nutt.—Eastern Oregon, Aug. 1914, H. F. Wilson, *3321;* Eugene, Lane Co., July 20, 1914, F. D. Bailey, *1504;* Portland, Aug. 21, 1915, E. Bartholomew, *5939* (Barth. Fungi Columb. *5048*); Sumpter, Baker Co., June, 1913, J. R. Weir, *91;* Grant's Pass, Josephine Co., Sept. 3, 1916, J. R. Weir, *249;* Hood River Co., July 22, 1915, *3138*.

*Artemisia rigida* (Nutt.) A. Gray—Eastern Oregon, 3,500 ft. altitude, Sept. 1900, W. C. Cusick, *2504;* Lost Valley, Wheeler Co., Sept. 9, 1894, J. B. Lieburg, *888*.

*Artemisia tridentata* Nutt.—Redmond, Crook Co., Sept. 15, 1913, Kirk Whited, *3187*, July 2, 1914, *2555;* Sherman, Sherman Co., July 1, 1914, *1938;* Umatilla, Umatilla Co., July 11, 1914, *1293*, May 11, 1915, *3038;* Park, Union Co., Oct. 9, 1897, E. P. Sheldon, *9113*.

This species, presumably a brachy-form, though no pycnia have yet been observed, is not to be confused with any other species on this host genus. The only other species recognized in North America is *P. conferta* (cf. 90) which is a micro-form.

59. **Puccinia abundans** (Pk.) comb. nov.

*Aecidium abundans* Pk. Bot. Gaz. **3**: 34. 1878.

*Puccinia Crandallii* Pam. & Hume, Proc. Dav. Acad. Sci. **7**: 250. 1899.

*Puccinia Kreageri* Ricker, Jour. Myc. **11**: 114. 1905.

On Caprifoliaceae: I.

*Symphoricarpos albus* (L.) Blake—Head of Applegate Creek, Jackson Co., July 29, 1913, E. P. Meinecke, *Cr D (1) 5;* Bridal Veil, Multnomah Co., May 18, 1915, *3054*, Mary's Peak, Benton Co., May 21, 1915, *3036;* Hilgard, Union Co., July 9, 1914, *2546;* Hood River, May 14, 1914, *2566*, July 21, 1915, *3063;* Springbrook, Yamhill

Co., May 14, 1914, F. D. Bailey, *2567;* Philomath, April 26, 1914, *2572;* Corvallis, April 28, 1915, *2612;* Grant's Pass, Josephine Co., Sept. 3, 1916, J. R. Weir, *181.*

On Poaceae: II and III.

*Festuca confinis* Vasey (*Poa Kingii* S. Wats.)—Steins Mts., Harney Co., July 2, 1896, J. B. Leiberg, *2945.*

*Festuca idahoensis* Elmer—Hilgard, Union Co., July 10, 1914, *1358, 1362;* Redmond, Crook Co., July 2, 1914, *1424, 1430.*

*Festuca rubra* L.—Hilgard, Union Co., July 10, 1914, *1366;* Mary's Peak, Benton Co., Aug. 15, 1914, *1571, 1573;* Newport, Lincoln Co., July 18, 1915, *3207.*

*Festuca subulata* Trin.—Ashland, Jackson Co., Sept. 10, 1914, *1563.*

The connection between this common western form on *Festuca* with *Aecidium abundans* was shown by Arthur in 1910 (Mycologia 4: 27. 1912). In three trials, using telial material on *F. confinis*, collected in Colorado and Utah, infection resulting in pycnia and aecia on *Symphoricarpos racemosus* was obtained.

60. Puccinia Acetosae (Schum.) Koern. Hedwigia **15**: 184. 1876.

*Uredo Acetosae* Schum. Enum. Pl. Saell. **2**: 231. 1803.

On Polygonaceae:

*Rumex acetosella* L.—Maples Station, Tillamook Co., Sept. 15, 1915, F. D. Bailey, *3102;* Corvallis, Oct. 19, 1915, G. B. Posey, *3000.*

This species has been recorded previously from North America only from Florida on *R. hastatulus* (Holway, North Am. Ured. 1: 35. 1906). Specimens on that host referred to this species are in the Arthur herbarium also from S. Carolina and Massachusetts and on *R. acetosella* from Massachusetts, Florida, New York and Indiana. All the specimens bear uredinia only. It is possible that some or all of the material should be referred to *Uromyces Acetosae* Schroet., as the two species are indistinguishable in the uredinial stage.

61. Puccinia ambigua (Alb. & Schw.) Lagerh., in Bubak, Sitz. Ver. Bohm. Ges. Wiss. 1898, **28**: 14. 1898.

*Aecidium Galii ambiguum* Alb. & Schw. Consp. Fung. 116. 1805.

*Puccinia difformis* Kunze, Myc. Hefte 1: 71. 1817.

*Allodus ambigua* Arth. Résult Sci. Congr. Bot. Vienne 345. 1906.

On Rubiaceae:

*Galium aparine* L.—Wren, Benton Co., June 26, 1914, *1330;* Ashland, Jackson Co., Sept. 10, 1914, *3096.*

This species possesses aecia and telia only in the life cycle. It has been studied by Bubak (l. c.) who found that primary aecia were followed by secondary aecia. Later Trebaux (Flora **81**: 394–404. 1895) repeated this observation and conducted culture work con-

firming Bubak's contention. This species should not be confused with *P. punctata* Lk. (cf. 156) which occurs on the same host from this region.

62. Puccinia Angelicae (Schum.) Fckl. Symb. Myc. 52. 1869. (Not *P. Angelicae* E. & E. 1884.)

*Uredo Angelicae* Schum. Enum. Pl. Saell. **2**: 233. 1803.

*Puccinia Archangelicae* Blytt, Christiania Vid. Selsk. Forhandl. No. 6: 51. 1896.

*Bullaria Angelicae* Arth. Résult Sci. Congr. Bot. Vienne 346. 1906.

On Umbelliferae:

*Angelica genuflexa* Nutt.—Woodburn, Clackamas Co., Sept. 1885, Thomas Howell.

*Angelica Lyallii* Wats.?—Larch Mt., Multnomah Co., Aug. 10, 1910, *2613*.

This species is evidently rare in North America having been reported otherwise only from a single collection from Washington on *A. genuflexa* and one from New York on *A. atropurpurea*. It is a brachy-form though pycnia have not been seen in American collections. This species has smooth teliospores and is easily separable from *Puccinia Ellisii* (cf. 98) on the same hosts from our region, which has verrucose spores.

63. Puccinia anomala Rost. Thümen, Flora **1877**: 92. 1877.

*Puccinia straminis simplex* Koern. Land. u. Forstw. Zeit. no. 50. 1865.

*Puccinia Hordei* Otth. Mitt. Nat. Ges. Bern. **1870**: 114. 1871. (Not *P. Hordei* Fckl. 1860.)

*Puccinia simplex* Erikss. & Henn. Getreideroste 238. 1896. (Not *P. simplex* Peck. 1881.)

*Aecidium Ornithogalum* Bubak, Ann. Myc. **3**: 223. 1905.

On Poaceae: II, III.

*Hordeum montanense* Schribn.—Corvallis, July 26, 1914, *1414*.

*Hordeum murinum* L.—Corvallis, July 8, 1914, G. B. Posey, *1354*.

*Hordeum nodosum* L.—Corvallis, July 26, 1914, *3257*.

*Hordeum vulgare* L.—Corvallis, July 6, 1914, *1683*, Aug. 13, 1914, *1691*, *1708*.

This, the leaf rust of barley, is evidently very common in Oregon, much more so than the collections listed above would indicate. It is evidently not abundant in America except on the Pacific coast. In the Arthur herbarium, specimens on wild barleys are represented only from Oregon, California and Utah. On the cultivated barley specimens are at hand only from California, Iowa and Wisconsin. It is

evidently spreading into the eastern United States as the writer collected it in August, 1916, at Ithaca and Savanna, New York.

Tranzschel has shown that this rust in Russia has its aecia on *Ornithogalum umbellatum* and *O. narbonense* (Mycol. Cent. 4: 70. 1914).

64. Puccinia Antirrhini Diet. & Holw. Hedwigia **36**: 298. 1897.
On Scrophulariaceae:

*Antirrhinum majus* L.—Portland, Aug. 1909, comm. Charles Ladd, *1080*, Aug. 28, 1914, comm. P. C. Schmeir, *1914;* Salem, Marion Co., July, 1911, comm. Mrs. Lord, *1127;* Corvallis, June 26, 1912, *1085*, Aug. 1912, *1025*.

The snapdragon rust is very common in Oregon both in gardens and in the greenhouse. For a long time it was known to occur only in California. As snapdragons came to be used more commonly in greenhouse culture the rust has gradually spread through the distribution of cuttings, till at the present time it is known to occur in most of the central and eastern states.

65. Puccinia arnicalis Pk. Bot. Gaz. **6**: 227. 1881.
On Carduaceae:

*Arnica cordifolia* Hook.—Near Aneroid Lake, July 1, 1899, II, E. R. Lake, *1497*.

A very distinct species having minutely verrucose teliospores, not thickened at the apex, and is known only from the Rocky mountain and Pacific coast regions.

66. Puccinia asarina Kunze, in Kunze & Schmidt, Myk. 1: 70. 1817.

*Puccinia Asari* Link in Willd. Sp. Pl. $6^2$: 68. 1825.

*Dicaeoma asarinum* Kuntze, Rev. Gen. Pl. 3: 467. 1898.
On Aristolochiaceae:

*Asarum caudatum* Lindl.—Portland, Aug. 30, 1915, E. Bartholomew, *5977* (Barth. Fungi Columb. *4840*).

This micro-form is known from North America on the above host, otherwise only from California, Idaho and Washington.

67. Puccinia asperifolii (Pers.) Wettst. Verh. Zool.-Bot. Ges. Wien **35**: 541. 1885.

*Aecidium asperifolii* Pers. Obs. Myc. 1: 97. 1796.

*Puccinia dispersa* Erikss. Zeitsch. f. Pflanzenkr. 4: 257. 1894.
On Poaceae:

*Secale cereale* L.—Hood River, June 19, 1914, *1402;* Corvallis, July 28, 1914, *1682;* Bend, Crook Co., Sept. 11, 1916, J. R. Weir, *243*.

The leaf rust of rye is evidently common throughout the state.

This species has its aecia on species of *Anchusa* and *Lycopsis* in Europe as was first shown by De Bary (Monatsber. k. Akad. d. Wiss. Berlin 211. 1866). No aecia referable to this species have been found in America, but Arthur (Mycologia 1: 236. 1909) obtained the development of pycnia on *Lycopsis arvensis* secured from Europe, following exposure to germinating telia on rye collected in Indiana. This culture indicates that the European and American rusts are identical.

68. Puccinia asperior E. & E. Bull. Washb. Lab. 1: 3. 1884.
*Puccinia oregonensis* Earle, Bull. N. Y. Bot. Gard. 2: 349. 1902.
*Allodus oregonensis* Arth. Résult Sci. Congr. Bot. Vienne 345. 1906.
*Allodus asperior* Orton, Mem. N. Y. Bot. Gard. 6: 193. 1916.
On Umbelliferae:
*Leptotaenia dissecta* Nutt.—Corvallis, June and July, 1898, M. Craig, April 14, 1899, M. Craig, June, 1910, *2614*, March 24, 1914, G. B. Posey, *2665;* Mary's River near Wren, Benton Co., June 5, 1915, *2673*.
This is one of the most common and conspicuous of rusts, probably widely distributed throughout western Oregon. The type of *P. oregonensis*, the second collection listed, was described as on *Sanicula bipinnata*, which is clearly an error for the above host as was first pointed out by Holway (N. Am. Ured. $1^4$: 93. 1913).

69. Puccinia Asterum (Schw.) Kern, Mycologia 9: 224. 1917.
*Aecidium asterum* Schw. Schrift. Nat. Ges. Leipzig 1: 67. 1822.
*Aecidium Solidaginis* Schw. Schrift. Nat. Ges. Leipzig 1: 68. 1822.
*Caeoma asteratum* Link in Willd. Sp. Pl. $6^2$: 51. 1825.
*Caeoma* (*Aecidium*) *erigeronatum* Schw. Trans. Am. Phil. Soc. II. 4: 292. 1832.
*Puccinia extensicola* Plowr. Brit. Ured. Ustil. 181. 1889.
*Puccinia Caricis-Erigerontis* Arth. Jour. Myc. 8: 53. 1902.
*Puccinia Caricis-Asteris* Arth. Jour. Myc. 8: 54. 1902.
*Puccinia Caricis-Solidaginis* Arth. Bot. Gaz. 35: 21. 1903.
On Carduaceae: I.
*Aster* sp.—Philomath, May 10, 1914, *1309, 3066;* Hilgard, Union Co., July 10, 1914, *3056;* Corvallis, May 9, 1914, *3367, 3368*, April 31, 1915, W. E. Lawrence, *3048;* Hood River, May 14, 1914, *3022;* Sumpter, Baker Co., June 1913, J. R. Weir, *85*.
*Erigeron speciosus* DC.—Near Whitewater ranger station, Mt. Jefferson, Aug. 16, 1914, H. P. Barss & G. B. Posey, *3292*.
*Euthamia occidentalis* Nutt.—Mary's River, Benton Co., June 1898, M. Craig.

On Cyperaceae: II and III.

*Carex athrostachya* Olney—Philomath, May 10, 1914, *3286*, Corvallis, June 29, 1914, G. B. Posey, *1333*.

*Carex canescens* L.—Hood River, Aug. 5, 1914, *3005*.

*Carex Deweyana* Schw.—Glendale, Douglass Co., Aug. 17, 1914, *1409;* Elk City, Lincoln Co., Aug. 20, 1914, *1381*, *1383;* Philomath, May 10, 1914, *3284;* Trail to Sulphur Springs, Benton Co., Nov. 3, 1912, *3288;* Corvallis, Apr. 29, 1914, F. D. Bailey, *3283*, May 19, 1913, *1193*.

*Carex festiva* Dewey—Newport, Lincoln Co., July 18, 1915, *3279*.

*Carex Goodenowii* J. Gay (*C. vulgaris* E. Fr.)—Hood River, June 20, 1914, *1405*.

*Carex phyllomanica* W. Boot?—Grant's Pass, Josephine Co., Sept. 3, 1916, J. R. Weir, *226*.

*Carex praegracilis* Boot (*C. marcida* Boot)—Corvallis, May 9, 1914, *3287*.

*Carex scoparia* Schk.—Corvallis, June 24, 1914, F. D. Bailey, *1386*.

*Carex stipata* Muhl.—Sherwood, Washington Co., July 10, 1914, F. D. Bailey, *1355;* Hood River, May 14, 1914, *3014;* Hubbard, Clackamas Co., May 27, 1914, *3011;* Portland, May 19, 1914, F. D. Bailey, *3003;* Corvallis, Aug. 10, 1910, *1189*, May 9, 1914, *3285*, July 29, 1915, *3281;* Eddyville, Lincoln Co., Aug. 8, 1915, Hoerner, *3356*.

*Carex straminea* Willd.—Hood River, July 24, 1915, *3280*.

*Carex subfusca* W. Boot.—Corvallis, July 29, 1914, *1444*.

*Carex* sp.—Ashland, Jackson Co., Sept. 10, 1914, *3008;* Corvallis, July 29, 1914, *1442;* Cottage Grove, Lane Co., July 14, 1914, *1350;* Philomath, Jan. 6, 1914, *1180*.

In 1901 Arthur (Jour. Myc. 8: 54. 1902) first began culture work showing that aecia which occur commonly on *Aster*, *Solidago* and related hosts are genetically connected with uredinia and telia on various species of *Carex*. The culture work conducted by Arthur is extensive and extends over a period of years from 1901–1914. In this series of culture work aecia have been produced on various species of *Aster*, *Solidago*, *Erigeron*, *Leptilon* and *Euthamia*, using telia from *Dulichium* and from many species of *Carex* from various parts of North America (Jour. Myc. 8: 54. 1902; 11: 58. 1905; 12: 15. 1906; 14: 13. 1908; Bot. Gaz. 35: 15, 21. 1903; Mycol. 1: 233. 1909; 2: 224. 1910; 4: 15, 16. 1912; 7: 70, 81. 1915). Fraser in 1911 (Mycol. 4: 181. 1912) confirms Arthur's results in part by successfully infecting *Aster acuminatus* using telial material from *Carex trisperma* L.

This study has also shown that the species as here considered is a composite form made up of several distinct physiological races.

The species is separable from all other American species of *Puccinia* on *Carex* by the presence of two pores in the upper part of the rather small (12–19 by 16–23 μ) urediniospores and the medium-sized (12–20 by 35–50 μ) teliospores.

The aecia of this species should not be confused with those of *P. stipae* (cf. 166), which occur on the same generic hosts and other Carduaceae in the west. In *P. Asterum* the aecia are cupulate, the peridium conspicuous, the spores globoid, nearly colorless and small (11–15 by 13–18 μ). In *P. stipae* the aecia occur on hypertrophied areas, the individual cups are gall-like and open by a central aperture, the peridium is evanescent, the spores are cinnamon brown, globoid, large (21–26 by 22–29 μ). The aecia of the latter species have not been found in Oregon, but doubtless occur abundantly in the eastern part of the state.

70. Puccinia Asteris Duby, Bot. Gall. **2**: 888. 1830.

On Carduaceae:

*Aster conspicuus* Lindl.—Hilgard, Union Co., July 10, 1914, *1538;* Crater Lake, Klamath Co., Sept. 3, 1916, J. R. Weir, *182.*

*Aster* sp.—Corvallis, Aug. 10, 1911, F. D. Bailey, *1175*, May 1, 1915, *3050;* Austin, Grant Co., June 1913, J. R. Weir, *102.*

71. Puccinia atro-fusca (Dudley & Thompson) Holway, Jour. Myc. **10**: 228. 1904.

*Uromyces atro-fuscus* Dudley & Thompson, Jour. Myc. **10**: 55. 1904.

On Cyperaceae:

*Carex Douglasii* Boot.—Enterprise, Wallowa Co., July 24, 1897, E. P. Sheldon (from Phan. spec. *8634*).

This species possesses amphispores which were first mistaken for the teliospores of a *Uromyces*. It may be distinguished from other *Carex* rusts by the presence of the amphispores together with the normal urediniospores, the latter are 20–26 μ long and thin walled, 1.5–2 μ thick. The aecial connection is unknown. It is known only from the Rocky mountain and Pacific coast regions.

72. Puccinia Balsamorrhizae Pk. Bull. Torrey Club **11**: 49. 1884.

*Trichobasis Balsamorrhizae* Pk. Bot. Gaz. **6**: 276. 1881.

On Carduaceae:

*Balsamorrhiza deltoidea* Nutt.—Corvallis, July 29, 1914, *1472;* Hermiston, Umatilla Co., May 12, 1915, *2663.*

*Balsamorrhiza sagittata* (Pursh) Nutt.—Hood River, Aug. 11, 1909, *3186;* Durfur, Wasco Co., June 19, 1914, *1836.*

73. Puccinia bicolor Ell. & Ev. Bull. Torrey Club **27**: 572. 1900.
On Cichoriaceae:

*Hieracium cinereum* Howell—Hood River, July 22, 1915, *3325*.

*Hieracium Scouleri* Hook.—White Pine, Baker Co., June 1913, J. R. Weir, *7*.

*Hieracium* sp.—Durfur, Wasco Co., June 30, 1914, *1338*.

This very distinct micro-form is known otherwise only from the type collection made at Waitsburg, Wash., May 7, 1900, on *H. Scouleri*, by R. M. Horner and distributed in E. & E. Fungi Col. *1570*.

74. Puccinia Bistortae (Strauss) DC. Fl. Fr. **6**: 61. 1815.

*Uredo Polygoni Bistortae* Strauss, Ann. Wett. Ges. **2**: 103. 1870.
On Polygonaceae:

*Polygonum imbricatum* Nutt.—Oregon?, Aug. 1880, Thos. Howell.

*Polygonum Newberryi* Small—Crater Lake, Klamath Co., Sept. 22, 1913, E. P. Meinecke, *Cr Pk D (2) 14;* N. slope Mt. Jefferson, 2,600 ft., Marion Co., Aug. 16, 1914, H. P. Barss & G. B. Posey, *1793*, Aug. 27, 1916, H. P. Barss, *3395*.

This species may be distinguished from other North American *Polygonum* rusts by the medium-sized teliospores (16–21 by 26–35 $\mu$) with wall of uniform thickness, without hyaline umbo. It is not known elsewhere in North America on the first mentioned host and otherwise only from Washington on *P. Newberryi*. Aecia are unknown.

75. Puccinia Blasdalei Diet. & Holw. Erythea **1**: 248. 1893.
On Alliaceae:

*Allium attenuifolium* Kellog—Corvallis, June 2, 1915, C. E. Owens, *2681*.

*Allium acuminatum* Hook.—Hood River Co., June 10, 1917, Leroy Childs.

This rust may be distinguished from other *Allium* rusts by the strongly developed stroma in the telial sori, and the tendency to form confluent telia covering large areas on the stems and leaves. The teliospores are large (16–26 by 40–61 $\mu$), thickened to 4–10 $\mu$ at the apex.

76. Puccinia Calochorti Pk. Bot. Gaz. **6**: 228. 1881.

*Allodus Calochorti* Arth. Résult Sci. Congr. Bot. Vienne 345. 1906.
On Liliaceae:

*Calochortus macrocarpus* Dougl.—Redmond, Crook Co., July 21, 1912, Kirk Whited, *3182;* Hills near Malheur River, Harney Co., June 6, 1901, W. C. Cusick, *2544;* Powder River Mts., Baker Co., Aug. 1896, C. V. Piper, *2460*.

All of the above specimens were secured from phanerogamic specimens, the first from the herbarium of the Oregon Agr. College, the others from the herbarium of the N. Y. Botanical Garden. The species is an opsis-form.

77. Puccinia Campanulae Carm. Smith's English Flora 5: 365. 1826.

*Puccinia Campanulae* Fckl. Sym. Myc. 53. 1869.

On Campanulaceae:

*Campanula Scouleri* Hook.—Mary's Peak, Benton Co., Aug. 15, 1914, *2559;* Hood River, July 24, 1914, *3023*.

A comparison of the above collections with European material shows that the rust is identical and should be referred as above. This is a micro-form unrecorded in America so far as the writer is aware, and known otherwise from North America only from collections made by the writer and others, on *C. rotundifolia* at Fall Creek, Ithaca, New York.

78. Puccinia Chelonis Diet. & Holw. Hedwigia 36: 297. 1897.

On Scrophulariaceae:

*Chelone nemorosa* Dougl.—Mt. Hood, Sept. 1, 1901, E. W. D. Holway.

A micro-form known otherwise only from Washington on the same host.

79. Puccinia Chrysanthemi Roze. Bull. Soc. Myc. Fr. 17: 92. 1900.

On Carduaceae:

*Chrysanthemum sinense* Sabine—Portland, Nov. 1914, W. H. Dunham, *1986*.

The above collection from a greenhouse is the only collection we have seen from Oregon. It is doubtless not infrequent in greenhouses throughout the state. The life history is unknown. This rust is evidently a native of Japan, having been introduced into America and Europe where it has become widespread on cultivated chrysanthemums.

80. Puccinia Cichorii (DC.) Bell, in Kickx. Fl. Fland. 2: 65. 1867.

*Uredo Cichorii* DC. Fl. Fr. 6: 74. 1815.

On Cichoriaceae:

*Cichorium intybus* L.—Corvallis, Sept. 21, 1914, G. B. Posey, *1931*.

81. Puccinia Cicutae Lasch, Klotsch. Herb. viv. myc. No. 787. 1845.

*Puccinia Cicutae* Thüm. Bull. Soc. Imp. des Nat. Moscow 52: 136. 1877.

On Umbelliferae:

*Cicuta occidentalis* Greene?—Klamath Falls, Klamath Co., Sept. 8, 1916, J. R. Weir, *223*.

*Cicuta* sp.—Eastern Oregon, June, 1885, T. Howell.

The last-mentioned specimen is from the herbarium of W. G. Farlow. It is marked on *Peucedanum*. The host is clearly *Cicuta* sp.

82. Puccinia Circaeae Pers. Roemer's Neues Mag. 1: 119. 1794.

On Onagraceae:

*Circaea pacifica* Asch. & Magn.—West of Noon station, Benton Co., Aug. 8, 1914, H. P. Barss, *1296;* Hood River, July 24, 1915, *3062;* Near Mary's Peak, Benton Co., Aug. 15, 1914, *3263;* Sumpter, Baker Co., July 16, 1913, J. R. Weir, *199*.

83. Puccinia Cirsii Lasch, in Rabh. Fungi Eur. No. 89. 1859.

*Puccinia inclusa* Syd. Monog. Ured. 1: 56. 1902.

On Carduaceae:

*Cirsium americanum* (Gray) Robinson—Wren, Benton Co., June 26, 1914, *1332;* Corvallis, May 20, 1915, *3242*.

*Cirsium edule* Nutt.—Elk City, Lincoln Co., Aug. 20, 1914, *2526*.

*Cirsium undulatum* (Nutt.) Spreng.—Sherman, Sherman Co., July 1, 1914, *1966*.

84. Puccinia claytoniata (Schw.) Pk. Bull. N. Y. State Mus. 6: 226. 1899.

*Caeoma* (*Aecidium*) *claytoniata* Schw. Trans. Am. Phil. Soc. II. 4: 294. 1832.

*Puccinia Mariae-Wilsoni* G. W. Clinton; Peck, Bull. Buff. Soc. Nat. Sci. 1: 66. 1873.

*Allodus claytoniata* Arth. Résult Sci. Congr. Bot. Vienne 345. 1906.

On Portulacaceae:

*Claytonia lanceolata* Pursh?—Austin, Grant Co., May, 1916, J. R. Weir, *206*.

85. Puccinia Clematidis (DC.) Lagerh. Tromsö Mus. Aarsh. 17: 47. 1895.

*Aecidium Clematidis* DC. Fl. Fr. 2: 243. 1805.

*Aecidium Aquilegiae* Pers. Icon. pict. IV. 58. 1806.

*Puccinia tomipara* Trel. Trans. Wis. Acad. Sci. 6: 127. 1885.

*Puccinia Agropyri* E. & E. Jour. Myc. 7: 131. 1892.

*Puccinia cinerea* Arth. Bull. Torrey Club 34: 583. 1907.

*Puccinia alternans* Arth. Mycol. 1: 248. 1909.

*Puccinia obliterata* Arth. Mycol. 1: 250. 1909.

On Ranunculaceae: I.

*Aquilegia formosa* Fish.—Myrtle Creek, Douglass Co., June 9, 1914, F. D. Bailey, *2573;* Hood River, May 14, 1914, *2565*, May 9, 1915, *3040;* Bridal Veil, Multnomah Co., May 18, 1915, *3051.*

*Aquilegia truncata* Fisch. & Mey.—Pokegama, Jackson Co., July 9, 1903, E. B. Copeland (Sydow, Ured. *1767*), E. B. Copeland, *3711* (Rocky Mt. Herb. *45896*).

*Clematis Drummondii* T. & G.—Freewater, Umatilla Co., July 10, 1914, *2562.*

*Clematis hirsutissima* Pursh (*C. Douglasii* Hook.)—Austin, Grant Co., July, 1913, J. R. Weir, *183.*

*Clematis ligusticifolia* Nutt.—Corvallis, Linn Co., Sept. 2, 1914, F. D. Bailey, *2563*, Benton Co., May 4, 1915, *3307.*

*Thalictrum occidentale* A. Gray—Corvallis, May 4, 1912, *1147*, July 4, 1914, G. B. Posey, *3067*, May 4, 1915, *3270;* Wren, Benton Co., June 26, 1914, *1331a;* White Pine, July, 1913, J. R. Weir, *153;* Austin, Grant Co., Aug. 1915, J. R. Weir, *205.*

On Poaceae: II, III.

*Agropyron dasystachyum* (Hook.) Vasey—Redmond, Crook Co., July 2, 1914, *1432.*

*Agropyron lanceolatum* Scribn. & Sm.—Redmond, Crook Co., July 2, 1914, *1427.*

*Agropyron spicatum* (Pursh) Rydb.—Wren, Benton Co., June 26, 1914, *1320.*

*Bromus carinatus* Hook. & Arn.—Newberg, Yamhill Co., June 8, 1913, F. D. Bailey, *1197;* Portland, July 10, 1905, J. J. Davis, Aug. 23, 1915, E. Bartholomew, (Barth. Fungi Columb. *4846*); Corvallis, Sept. 10, 1914, *1577;* Philomath, May 10, 1914, *3193;* Hood River, May 14, 1914, *1587*, *1588*, *1593;* Grant's Pass, Josephine Co., Sept. 3, 1916, J. R. Weir, *207.*

*Bromus carinatus californicus* Shear—Philomath, Jan. 6, 1914, *1148.*

*Bromus grandis* (Shear) Hitchc.—Corvallis, June 4, 1914, *1384.*

*Bromus hordeaceus* L.—Portland, May 21, 1914, *1582.*

*Bromus hordeaceus leptostachys* Beck.—Hood River, May 20, 1914, *1585;* Springbrook, Yamhill Co., May 14, 1914, F. D. Bailey, *1594*, *1595.*

*Bromus marginatus* Nees.—Hood River, Aug. 6, 1914, *1559*, July 27, 1915, *3192;* Corvallis, June 24, 1914, G. B. Posey, *1389*, June 29, 1914, G. H. Godfrey, *1312;* Rose City Park, Portland, Jan. 9, 1914, *1198;* Redmond, Crook Co., July 2, 1914, *1422;* Hilgard, Union Co., July 10, 1914, *1365.*

*Bromus secalinus* L.—Cottage Grove, Lane Co., July 14, 1914, *1352.*

*Bromus tectorum* L.—Clatskanie, Columbia Co., May 20, 1914, F. D. Bailey, *1581*.

*Bromus villosus* Forsk.—Myrtle Creek, Douglass Co., June 9, 1914, F. D. Bailey, *1406*.

*Bromus vulgaris* Shear—Ashland, Jackson Co., Sept. 10, 1914, *1569;* Corvallis, Feb. 14, 1914, *3261*, July 4, 1914, G. B. Posey, *1418*, July 29, 1914, *1443;* trail to Sulphur Springs, Benton Co., Nov. 3, 1914, *3195;* Mary's Peak, Benton Co., Sept. 15, 1914, *1574*.

*Elymus condensatus* Presl.—Albany, Linn Co., Aug. 1907, D. Griffiths.

*Elymus glaucus* Buckl.—Wren, Benton Co., June 26, 1914, *1321*, *1331;* Ashland, Jackson Co., Sept. 10, 1914, *1562*, *1564;* N. slope Mt. Hood, Aug. 7, 1914, *1556;* Mary's Peak, Benton Co., Aug. 15, 1914, *1575;* The Dalles, Wasco Co., July 1, 1914, *1341;* Garden Home, Multnomah Co., July 20, 1915, *3202;* Hood River, June 20, 1914, *1403*, Aug. 5, 1914, *3204;* Corvallis, Feb. 14, 1914, *3262;* June 29, 1914, G. B. Posey, *1304*, G. H. Godfrey, *1305*, July 29, 1914, *1439*, *1440*.

*Elymus triticoides* Buckl.—Columbia River, near mouth of Deschuttes River, Sherman Co., July 29, 1914, M. E. Peck.

*Poa ampla* Merrill—Hood River, July 22, 1915, *3259*.

*Puccinella Nuttalliana* (Schult.) Hitchc.—Grand Ronde Valley, Union Co., July, 1914.

*Sitanion californicum* J. G. Smith—N. slope Mt. Jefferson, Aug. 12, 1914, H. P. Barss, *1560*.

*Sitanion glabrum* J. G. Smith—Umatilla, Umatilla Co., July 11, 1914, *1370*.

*Sitanion jubatum* J. G. Smith—Redmond, Crook Co., July 2, 1914, *1428*.

*Sitanion velutinum* Piper—Hood River, July 22, 1915, *3255;* Hermiston, Umatilla Co., May 12, 1915, *3179*.

This common subepidermal species, as here considered, includes nearly if not all the forms having aecia on Ranunculaceous hosts.

Dietel (Oesterr. bot. Zeitschr. 42: 261. 1892) was apparently the first to culture this species. Klebahn (Die Wirtsw. Rostpilze 292. 1904) has presented a summary of Dietel's work together with that of other European investigators.

In America, Arthur has conducted extensive culture work beginning in 1904, using telial material from various parts of the country, on five different genera of grasses representing ten species, and has successfully cultured them on five genera of Ranunculaceae. His work indicates the presence of a number of well-marked races. (Jour. Myc. 11: 62. 1905, 13: 197. 1907, 14: 15. 1908; Mycologia 1: 246, 248, 249. 1909, 2: 225. 1910, 4: 54. 1912, 7: 73, 82. 1915, 8: 132. 1916.)

This species may be distinguished from other grass rusts having the telia long covered by the epidermis primarily on the urediniospore characters. They are not accompanied by paraphyses, the wall is moderately thin, 1.5–2 $\mu$, pale yellow to cinnamon brown, and the pores are scattered. The telia may or may not be surrounded by stromal hyphae and are rather narrow, 13–24 $\mu$.

86. Puccinia Clintonii Peck, Rept. N. Y. State Mus. **28**: 61. 1876.
On Scrophulariaceae:

*Pedicularis bracteosa* Benth.?—N. slope Mt. Jefferson, Aug. 16, 1914, H. P. Barss & G. B. Posey, *2545*.

*Pedicularis racemosa* Dougl.—N. slope Mt. Jefferson, 7,000 ft., Aug. 13, 1914, H. P. Barss, *2544*.

87. Puccinia Cnici Mart. Fl. Mosq. 226. 1817.

*Puccinia Cirsii-lanceolati* Schroet., Cohn, Krypt. Fl. Schl. $3^1$: 317. 1887.

On Carduaceae:

*Cirsium lanceolatum* (L.) Scop.—Corvallis, Oct. 21, 1911, F. D. Bailey, *1963*, Mar. 6, 1914, G. H. Godfrey & F. D. Bailey, *1965;* Elk City, Lincoln Co., Aug. 20, 1914, *1964;* The Dalles, Wasco Co., July 1, 1914, *1334;* Portland, Aug. 21, 1915, E. Bartholomew (Barth. Fungi Columb. *5053*).

88. Puccinia Comandrae Pk. Bull. Torrey Club **11**: 49. 1884.
On Santalaceae:

*Comandra umbellata* (L.) Nutt.—Dufur, Wasco Co., July 30, 1914, *2504;* Hood River, May 18, 1915, *2660*, July 22, 1915, *3141*.

This micro-form, found commonly in the Rocky Mt. and Pacific coast states, possesses teliospores having similar morphological characters to those of the heteroecious rust *P. pustulata* (Curt.) Arth., which has aecia on *Comandra* and uredinia and telia on *Andropogon*. A number of such correlations between micro-forms and the telia of heteroecious forms whose aecia occur on the same host have been pointed out by Travelbee (Proc. Ind. Acad. Sci. **1914**: 233. 1915) among species occurring in North America. Dietel (in Engler & Prantl, Die Nat. Pflanzenf. $1^{1**}$: 69. 1897) was apparently the first to point out this sort of correlation between *P. mesneriana* Thüm. and *P. coronata* (*P. Rhamni*).

89. Puccinia commutata Sydow, Monog. Ured. **1**: 201. 1902.

*Allodus commutata* Arth. Résult. Sci. Congr. Bot. Vienne 345. 1906.
On Valerianaceae:

*Valeriana occidentalis* Heller—Hilgard, Union Co., July 10, 1914, *1541*.

90. Puccinia conferta Diet. & Holw. Erythea 1: 250. 1893.
*Puccinia recondita* Diet. & Holw. Erythea 2: 128. 1894.
On Carduaceae:
*Artemisia ludoviciana* Nutt.—Corvallis, Sept. 2, 1914, F. D. Bailey, *2532*, Sept. 4, 1914, *2509*.
A micro-form in which the teliospores resemble quite closely those of *P. Absinthii* (cf. 58), a brachy-form also common in the west. It is probable that this should be considered a correlated form.

91. Puccinia Convolvuli (Pers.) Cast. Obs. 1: 16. 1842.
*Uredo Betae Convolvuli* Pers. Syn. Fung. 221. 1801.
On Convolvulaceae:
*Convolvulus atriplicifolius* (Hallier f.) House—Central Point, Jackson Co., Oct. 6, 1914, M. P. Henderson, *1949;* Grant's Pass, Josephine Co., Sept. 3, 1916, J. R. Weir, *221*.

92. Puccinia Crepidis-acuminatae Sydow, Oestr. Zeitschr. 51: 27. 1901.
On Cichoriaceae:
*Crepis gracilis* (D. C. Eaton) Rydberg—Baker City, Baker Co., July, 1913, J. R. Weir, *154*.

93. Puccinia Cyani (Schleich.) Pass. Rabh. Fungi Eur. No. 1767. 1874.
*Uredo Cyani* Schleich. Pl. Helv. 95.
On Carduaceae:
*Centaurea Cyanus* L.—Corvallis, June, 1913, *1145*, April 8, 1914, *2551*, July 29, 1914, *2552*, July 4, 1914, G. B. Posey, *3106;* Orenco, Washington Co., April 2, 1915, *3069*.

94. Puccinia DeBaryana Thüm. Flora 58: 364. 1875.
*Puccinia compacta* DeBary, Bot. Zeit. 16: 83. 1858. (Not *P. compacta* Berk. 1855.)
On Ranunculaceae:
*Anemone Drummondii* Wats.—Mt. Hood, 7,000 ft., foot of Eliott Glacier, Sept. 1, 1901, E. W. D. Holway.

95. Puccinia Dentariae (Alb. & Schw.) Fuckel, Symb. Mycol. Nachtr. 1: 7. 1871.
*Uredo Dentariae* Alb. & Schw. Consp. Fung. 129. 1805.
On Cruciferae:
*Dentaria tenella* Pursh—Corvallis, April 5, 1914, *1288*.
A micro-form occurring on the petioles and blades of the basal leaves causing considerable distortion. So far as the writer is aware this species is known from North America only from the above collection.

96. Puccinia Dichelostemmae D. & H. Erythea 3: 78. 1895.
*Allodus Dichelostemmae* Orton, Mem. N. Y. Bot. Gard. 6: 183. 1916.

On Alliaceae:

*Hookera pulchella* Salisb. (*Brodiaea congesta* Smith)—Dallas, Polk Co., March 20, 1900, W. N. Suksdorf (Barth. N. Am. Ured. *1541*); Corvallis, April 28, 1915, *2611*, May 1, 1915, *2669;* E. of Wren Station, Benton Co., April 17, 1915, *2618*.

The first-mentioned collection bears aecia and a few telia. It is probable that they belong together. The last specimen mentioned consists of aecia only. The others bear telia only. The two stages rarely occur together. This species may be separated from all other species of *Puccinia* occurring on Alliaceae by the very large, broad teliospores (38–45 by 43–58 $\mu$) having smooth walls 5–7 $\mu$ thick.

97. Puccinia Douglasii Ell. & Ev. Proc. Phil. Acad. 1893: 152. 1893.
*Puccinia Richardsonii* Sydow, Monog. Ured. 1: 317. 1902.
*Allodus Douglasii* Orton, Mem. N. Y. Bot. Gard. 6: 198. 1916.

On Polemoniaceae:

*Phlox condensata* (A. Gray) E. Nels.—N. slope Mt. Hood, 7,000 ft., Aug. 7, 1914, III, *1494*, I, *2624*.

*Phlox diffusa* Hook.—N. slope Mt. Hood, 7,000 ft., Aug. 7, 1914, *1602*, *1603;* Sept. 1, 1901, E. W. D. Holway.

98. Puccinia Ellisi DeToni, in Sacc. Syll. Fung. 7: 651. 1888.
*Puccinia Angelicae* E. & E. Bull. Wash. Lab. 1: 3. 1884. (Not *P. Angelicae* Fckl. 1869.)
*Puccinia Bakeriana* Arth. Bull. Torrey Club 31: 3. 1904.

On Umbelliferae:

*Angelica genuflexa* Nutt.—Corvallis, Sept. 7, 1901, E. R. Lake, *1496*.

Otherwise known only from Idaho and Washington on the above host, and from California on *A. tomentosa*. It is doubtless a brachyform, though no pycnia have been found. The teliospores are closely and finely verrucose, a character which enables one to distinguish this species easily from *P. Angelicae* (cf. 62).

99. Puccinia Epilobii-tetragoni (DC.) Wint. in Rabenh. Krypt. Fl. 1: 214. 1881.
*Uredo vagans* $\alpha$ *Epilobii-tetragoni* DC. Fl. Fr. 2: 238. 1805.
*Puccinia Gayophyti* Billings, in King, Geol. Expl. 40th Par. 5: 414. 1871.
*Puccinia Oenotherae* Vize, Grevillea 5: 109. 1877.
*Puccinia Boisduvaliae* Pk. Bot. Gaz. 7: 45. 1882.

*Puccinia Clarkiae* Pk. Bull. Torrey Club 11: 49. 1884.

*Puccinia glabella* Holw. N. Am. Ured. 1: 76. 1907.

On Onagraceae:

*Boisduvalia densifolia* (Lindl.) Wats.—Minam River, Wallowa Co., Oct. 2, 1897, E. P. Sheldon, *9049;* Corvallis, July, 1910, *1116*, Aug. 10, 1911, *1123*, Sept. 20, 1914, *1546;* Calapooya Valley, Douglas Co., July 24, 1899, M. A. Barber (Rocky Mt. Herb. *40989*); Grant's Pass, Josephine Co., Sept. 2, 3, 1916, J. R. Weir, *222*, *251*.

*Boisduvalia glabella* (Nutt.) Walp.—Burns, Harney Co., Aug. 1901, Griffiths & Morris (Griffiths, W. Am. Fungi *385*).

*Boisduvalia stricta* (A. Gray) Greene—Corvallis, Aug. 13, 1914, *1492;* Medford, Jackson Co., June 26, 1915, G. B. Posey, *3275;* Wimer, Jackson Co., July 22, 1892, E. W. Hammond, *149* (Rocky Mt. Herb. *48696*).

*Clarkia pulchella* Pursh—Hilgard, Union Co., July 10, 1914, *1529*.

*Epilobium minutum* Lindl.—Corvallis, Aug. 15, 1909, *1170*.

*Epilobium paniculatum* Nutt.—Cole's Creek, Wallowa Co., June 10, 1897, E. P. Sheldon, *8263* (Rocky Mt. Herb. *70411*); Hood River, May 14, 1914, *1510*, May 16, 1915, *3271;* Hilgard, Union Co., July 10, 1914, *1530*, *1544;* Ontario, Mahheur Co., Aug. 1901, Griffiths & Morris (Griffiths, W. Am. Fungi *383*); Corvallis, Aug. 1910, *3065*, Aug. 10, 1911, F. D. Bailey, *1174;* The Dalles, Wasco Co., June 19, 1914, *3107;* N. slope Mt. Hood, Aug. 7, 1914, *1491;* Near Cascade Locks, Hood River Co., Aug. 11, 1910, *1073;* Philomath, May 26, 1914, *3351*, April 21, 1899, Moses Craig; Klamath Falls, Klamath Co., Sept. 8, 1916, J. R. Weir, *225*.

*Gayophytum ramossissimum* T. & G.—Redmond, Crook Co., July 1, 1914, *2536;* Hood River, July 23, 1915, *3272;* Farewell Bend, Crook Co., July 15, 1894, J. B. Lieberg, *435* (Rocky Mt. Herb. *66228*).

*Godetia amoena* (Lihm.) Lilja.—Corvallis, July, 1910, *1115*, Wren, Benton Co., June 26, 1914, *1327*.

*Sphaerostigma Boothii* (Dougl.) Walp.—Muddy Station, John Day Valley, May 12, 1885, Thomas Howell.

*Sphaerostigma dentatum* (Cav.) Walp.—Pleasant Creek, near Wimer, Jackson Co., April 23, 1889, E. W. Hammond, *143*.

As here considered, this species includes all the long-cycled autoecious forms occurring on Onagraceae. The treatment follows the disposition made of them by Bisby in his recent admirable discussion of the Onagraceous rusts (Amer. Jour. Bot. 3: 538. 1916).

100. Puccinia epiphylla (L.) Wettst. Verhl. Zool.-Bot. Ges. Wein. 35: 541. 1885.

*Lycoperdon epiphyllum* L. Sp. Pl. 1653. 1753.

*Aecidium Tussilaginis* Pers. in Gmel. Syst. Nat. 2: 1473. 1791.

*Puccinia Poarum* Niels. Bot. Tidsskr. II. 3: 26. 1877.

On Poaceae:

*Poa ampla* Merrill—Hood River, May 14, 1914, *1591*.

*Poa annua* L.—Hood River, July 22, 1915, *3196*.

*Poa macrantha* Vasey—Newport, Lincoln Co., June 20, 1915, *3123*.

*Poa pratensis* L.—Corvallis, May 19, 1913, F. D. Bailey, *1194*, March 29, 1914, G. B. Posey, *3126*, April 29, 1914, F. D. Bailey, *3125*, June 29, 1914, G. B. Posey, *1311;* Philomath, May 10, 1914, *3124;* Hood River, May 14, 1914, *1586*, *1592;* The Dalles, Wasco Co., July 1, 1914, *1302;* N. slope Mt. Hood, Aug. 7, 1914, *1557;* Ashland, Jackson Co., Sept. 10, 1914, *1565;* Kamela, Union Co., July 22, 1915, M. E. Peck; Klamath Falls, Klamath Co., Sept. 8, 1916, J. R. Weir, *224*, *239*.

*Poa triflora* Gilib.—Klamath Falls, Klamath Co., Sept. 8, 1916, J. R. Weir, *239a*.

*Poa* sp.—Grant's Pass, Josephine Co., Sept. 3, 1916, J. R. Weir, *228*, *229;* Klamath Falls, Klamath Co., Sept. 8, 1916, J. R. Weir, *218;* Austin, Grant Co., Aug. 1915, J. R. Weir, *194*.

This rust is especially common in western Oregon particularly on blue grass. Only uredinia are known in the above collections as is the common condition except in those made in the far north or at high elevations.

Nielsen (Bot. Tidsskr. 2: 26. 1877) was the first to show the relation between this rust and *Aecidium Tussilaginis* Gmel. He succeeded in infecting *P. annua*, *P. trivialis*, *P. nemoralis*, *P. fertilis* and *P. pratensis* by sowing aeciospores from *Tussilago farfara*. He infected the aecial host by sowing with teliospores from *P. annua*.

Additional observations and culture work have been recorded by various European authors, which have been summarized by Klebahn (Die Wirtsw. Rostp. 290. 1904).

101. Puccinia Eriophori Thüm. Bull. Soc. Imp. Nat. Moscow 55: 208. 1880.

*Aecidium Ligulariae* Thüm. Nov. Giorn. Bot. Ital. 12: 196. 1880.

*Aecidium Cinerariae* Rostr. Overs. Kong. Dansk. Vid. Selsk. Forh. Koph. 1884–5: 17. 1884.

On Carduaceae: I.

*Senecio ductaris* Piper—Alpine meadow, E. Mt. Hood, 5,000 ft., July 23, 1915, *3326*.

On Cyperaceae: III.

*Eriophorum polystachyon* L.—Alpine meadow, E. Mt. Hood, 5,000 ft., July 23, 1915, *3331*.

In the alpine meadow where the above collections were made the *Aecidium* was very abundant and in fine condition. A search was

made for overwintered telia on Cyperaceous hosts associated with the *Senecio* and the only rust found was on very much weathered leaves which have been determined by comparison of the microscopic structure as above indicated.

Tranzschel (Beitr. Biol. Ured. III: 4. 1907), working in Russia, was the first to culture this species. He used telial material on *Eriophorum angustifolium* to successfully infect *Ligularia sibirica* and *Senecio paluster.*

In America, Arthur (Mycol. 8: 131. 1916), using aecial material from New York on *Senecio aureus*, obtained successful infection resulting in uredinia and telia on *E. viridi-carinatum.*

102. **Puccinia Eriophyllii** sp. nov.

O. and I. Pycnia and aecia unknown.

II. Uredinia amphigenous and caulicolous, scattered, small, roundish, 0.3–0.6 mm. across, early naked, pulverulent, pulvinate, chestnut brown, surrounding epidermis not conspicuous; urediniospores globoid, obovoid or oblong, 21–27 by 26–29 $\mu$, wall chestnut brown, 2–3 $\mu$ thick, moderately and finely echinulate, pores 2, approximately equatorial.

III. Telia amphigenous, scattered, small, round, 0.3–0.6 mm. across, early naked, compact, pulvinate, blackish brown, ruptured epidermis not conspicuous; teliospores ellipsoid to oblong, 18–21 by 26–30 $\mu$, apex and base rounded, not constricted, wall chestnut brown, 2–2.5 $\mu$ thick, uniform, minutely and obscurely verrucose; pedicel colorless, deciduous.

On Carduaceae:

*Eriophyllum lanatum* (Pursh) Forbes—Wren, Benton Co., June 26, 1914, *1319* (type).

*Eriophyllum leucophyllum* (DC.) Rydberg—Redmond, Crook Co., July 1, 1914, *3083*.

Distinguished from other species of *Puccinia* on related hosts by the very small teliospores.

103. **Puccinia Fendleri** (Tracy & Earle) comb. nov.

*Aecidium Fendleri* Tracy & Earle, in Green, Pl. Baker 1: 17. 1901.

*Puccinia Koeleriae* Arth. Mycologia 1: 247. 1909.

On Berberidaceae: I.

*Berberis aquifolium* Pursh—Corvallis, May 12, 1914, *1276*, June 7, 1908, J. C. Bridwell, *3389*.

*Berberis nervosa* Pursh—Hilgard, Union Co., July 10, 1914, *2568*.

On Poaceae:

*Koeleria cristata* (L.) Pers.—Hilgard, Union Co., July 10, 1914, *1363*.

The aecia of this species have often been confused with those of *P. graminis* (cf. 151). Arthur in 1908 (Mycol. 1: 246. 1907), using telial material from *Koeleria cristata* from Colorado, obtained, as a result of infection experiments, the development of aecia on *Berberis aquifolium*.

104. PUCCINIA GEMELLA Diet. & Holway, in Sydow's Monog. Ured. 1: 541. 1903.

ON RANUNCULACEAE:

*Caltha biflora* DC.—N. slope Mt. Jefferson, 6,000 ft., Aug. 13, 1914, H. P. Barss & G. B. Posey, *1624*; foot of Mt. Jefferson, 5,000 ft., Aug. 28, 1916, H. P. Barss, *3401*.

A micro-form, differing from *P. Treleasiana* Pazsch., which occurs in the Rocky Mt. region on *Caltha* sp., in the smooth spores.

105. PUCCINIA GENTIANAE (Strauss) Link, in Willd. Sp. Pl. $6^2$: 73. 1825.

*Uredo Gentianae* Strauss, Ann. Wett. Ges. 2: 102. 1810.

ON GENTIANACEAE:

*Gentiana oregana* Engelm.—Sumpter, Baker Co., July 16, 1913, J. R. Weir, *191*.

106. PUCCINIA GILIAE Hark. Bull. Cal. Acad. 1: 34. 1884.

ON POLEMONIACEAE:

*Navarettia intertexta* (Benth.) Hook.—Corvallis, Aug. 1898, Moses Craig, July, 1910, *1121;* Umpqua Valley, Douglass Co., June, 1887, Thomas Howell, *1835;* Hood River, Aug. 17, 1888, L. F. Henderson (*673*), *1120*.

This is a hemi-form distinct from *P. plumbaria* (cf. 150) which is an opsis-form. In *P. Giliae* the telia are early naked and the spores smooth. In *P. plumbaria* the telia are long covered by the cinereous epidermis and the spores are finely and closely verrucose.

107. PUCCINIA GLUMARUM (Schmidt.) Erikss. & Henn. Zeits. Pflanzenkr. 4: 197. 1894.

*Uredo glumarum* Schmidt. Allg. Oekon. Fl. 1: 27. 1827.

*Puccinia neglecta* West. Bull. Soc. Bot. Belg. 2: 248. 1863.

*Trichobasis glumarum* Lev.; Cooke, Myc. Fung. 208. 1865.

ON POACEAE:

*Elymus glaucus* Buckl.—Hood River Co., May 14, 1914, *1590*, *1596*, *1597*, July 23, 1915, *3199*.

*Hordeum Gussoneanum* Parl.—Corvallis, June 4, 1914, F. D. Bailey, *1385*.

*Hordeum vulgare* L.—Moro, Sherman Co., June 11, 1915, F. K Ravn and A. G. Johnson.

*Sitanion hystrix* (Nutt.) J. S. Smith—Redmond, Crook Co., July 1, 1914, *1423*, *1429*.

*Sitanion jubatum* J. G. Smith—Ashland, Jackson Co., June 7, 1916, H. B. Humphrey; Klamath Falls, Klamath Co., Sept. 11, 1916, J. R. Weir, *232*.

*Triticum aestivum* L.—Moro, Sherman Co., June 25, 1915, D. E. Stephens, *3371*, *3379;* Medford, Jackson Co., June 8, 1915, F. K. Ravn, A. G. Johnson, *3370*.

*Triticum compactum* Host.—Moro, Sherman Co., June 11, 1915, F. K. Ravn & A. G. Johnson (Barth. Fungi Columb. *4756*); June 25, 1915, D. E. Stephens, *3373*, *3378*, *3380*, *3385*.

*Triticum diococcum* L.—Moro, Sherman Co., June 11, 1915, F. K. Ravn & A. G. Johnson.

*Triticum vulgare* L. (Collective)—Corvallis, June 10, 1915, *2676*, *2679*, *2680*, June 12, 1915, *3134;* Hood River, July 22, 1915, *3142;* Moro, Sherman Co., June 11, 1915, F. K. Ravn, A. G. Johnson, M. A. Carleton.

This very important wheat rust was first found in the United States, May 21, 1915, at Sacaton, Arizona, by Dr. F. K. Ravn, the eminent Danish cereal pathologist, who at that time was making a tour of investigation of cereal diseases in company with pathologists of the Department of Agriculture (Carleton, Science N. S. 42: 58. 1916). A few weeks later the rust was found by Dr. Ravn and party at Medford and Corvallis and later was detected at Moro, Oregon. There is every evidence that this rust has been present in the western states for some years. Several collections reported above were made in 1914 but were confused with *P. Clematidis*. The writer is indebted to Dr. H. B. Humphrey for examining most of the collections and for the detection of several specimens belonging here, previously referred to other species.

108. Puccinia granulispora Ell. & Gall.; Ellis & Ever. Bull. Torrey Club 22: 61. 1895.

On Alliaceae:

*Allium nevii* Wats.?—Austin, Grant Co., Aug. 1915, J. R. Weir, *204*.

109. Puccinia Grossulariae (Schum.) Lagerh. Tromsø. Mus. Aarsh. 17: 60. 1895.

*Aecidium Grossulariae* Schum. Pl. Enum. Saell. 2: 223. 1803.

*Puccinia Pringsheimiana* Kleb. Zeits. für Pflanzenkr. 4: 194. 1894.

*Puccinia Magnusii* Kleb. Zeits. für Pflanzenkr. 5: 79. 1895.

*Puccinia albiperidium* Arth. Jour. Myc. 8: 53. 1902.

*Puccinia uniporula* Orton, Mycol. 4: 201. 1912.

On Grossulariaceae: I.

*Ribes divaricatum* Dougl.—Bridal Veil, Multnomah Co., May 18, 1915, *3252;* Hilgard, Union Co., July 10, 1914, *3001.*

*Ribes lacustre* (Pers.) Poir.—N. slope Mt. Hood, Aug. 7, 1914, *2561.*

*Ribes sanguineum* Pursh—Bridal Veil, Multnomah Co., May 18, 1915, *3253.*

*Ribes* sp.—Philomath, April 26, 1914, *2571;* Corvallis, April 11, 1915, *3045.*

On Cyperaceae: II, III.

*Carex festiva* Dewey—Hilgard, Union Co., July 10, 1914, *1360.*

*Carex Goodenowii* J. Gay—Hilgard, Union Co., July 10, 1914, *1359.*

*Carex Kelloggii* W. Boot—Portland, Aug. 21, 1915, E. Bartholomew *5941* (Barth. Fungi Columb. *4962*).

*Carex magnifica* Dewey—Clatsop Co., Nov. 7, 1913, *1195.*

*Carex mertensii* Prescott—Mt. Hood, Aug. 7, 1914, *3004.*

*Carex monile* Tuckerm.—Clatskanie, Columbia Co., May 20, 1914, F. D. Bailey, *3013.*

*Carex nebraskensis* Dewey—Hilgard, Union Co., July 10, 1914, *1361.*

*Carex phyllomanica* W. Boot?—Klamath Falls, Klamath Co., Sept. 8, 1916, J. R. Weir, *254.*

*Carex spectabilis* Dewey—W. slope Mt. Jefferson, July 3, 1914, F. D. Bailey, *1417;* Vicinity Mt. Jefferson, Aug. 12, 1914, H. P. Barss & G. B. Posey, *3007.*

*Carex* sp.—In open meadow along Minum River, Wallowa Co., Aug. 20, 1897, E. P. Sheldon, *8751.*

This common form having aecia on *Ribes* sp. was first cultured by Klebahn in 1892. The species has since been extensively studied by the culture method in both Europe and America (Klebahn, Die Wirtsw. Rostp. 295–302. 1904) under various names.

In America, Arthur began culture work in 1901 and has reported the results of numerous cultures (Jour. Myc. 8: 53. 1902; 10: 11. 1904; 11: 59. 1905; 12: 65. 1906; 13: 196. 1907; 14: 13. 1908; Mycol. 4: 13. 1912; 7: 67. 1915; 7: 78. 1915). The species is doubtless represented by several biological strains and further culture work will need to be conducted in order to determine their limits. Considerable confusion has resulted on account of the variable number and position of the germ pores in the urediniospores.

110. Puccinia grumosa Syd. & Holw. in Sydow, Monog. Ured. 1: 641. 1903.

On Liliaceae:

*Stenanthium occidentale* A. Gray—Bridal Veil, Multnomah Co., May 18, 1915, *2670;* Hood River, July 24, 1915, *3082.*

This species, described from a collection on *Zygadenus elegans* made by Professor Holway at Banff, Alberta, has been previously known only from the original collection. The above collections clearly belong here and add a new host. The only other collection of *Puccinia* on *Stenanthium* known to the writer is one obtained by him in January, 1917, on a phanerogamic specimen of *S. gramineum* collected in Georgia by A. W. Curtis, now in the herbarium of the New York Botanical Garden. This has been referred to *P. atropuncta*, a species known only from east of the Rocky mountains on related hosts.

111. Puccinia Harknessi Vize, Grevillea 7: 11. 1878.

*Puccinia cladophila* Pk. Bot. Gaz. 4: 127. 1879.

On Cichoriaceae:

*Lygodesmia juncea* (Pursh) D. Don—Denio, Harney Co., Aug. 1901, Griffiths & Morris (Griffiths, W. Am. Fungi *396c*).

*Ptiloria paniculata* (Nutt.) Green—Sherman, Sherman Co., July 1, 1914, *2535*.

112. **Puccinia Helianthi-mollis** (Schw.) comb. nov.

*Aecidium Helianthi-mollis* Schw. Schrift. d. Nat. Ges. Leipzig 1: 68. 1822.

*Puccinia Helianthi* Schw. Schrift. d. Nat. Ges. Leipzig 1: 73. 1822.

On Carduaceae:

*Helianthus annuus* L.—Sherman, Sherman Co., July 1, 1914, *2525;* Corvallis, Aug. 1910, F. D. Bailey, *1129;* Umatilla, Umatilla Co., July 11, 1914, *1468*.

113. Puccinia Hemizoniae Ell. & Tracy, Jour. Myc. 7: 43. 1891.

On Carduaceae:

*Hemizonia truncata* (DC.) Gray—Grant's Pass, Josephine Co., July 12, 1887, Thos. Howell.

*Lagophylla ramossissima* Nutt.—Grant's Pass, Josephine Co., Sept. 2, 1916, J. R. Weir, *220*.

114. Puccinia Heucherae (Schw.) Diet. Ber. der Deutsch. Bot. Ges. 9: 42. 1891.

*Uredo Heucherae* Schw. Schrift. Nat. Ges. Leipzig 1: 71. 1822.

*Puccinia Tiarellae* B. & C. Grevillea 3: 53. 1874.

*Puccinia spreta* Pk. Rep. N. Y. State Mus. 29: 67. 1878.

*Puccinia congregata* E. & H. Bull. Calif. Acad. Sci. 1: 26. 1884.

On Saxifragaceae:

*Heuchera micrantha* Dougl.—Hood River, Feb. 1, 1915, *3266;* Mary's River, Corvallis, June 5, 1915, *2674;* Ashland, Jackson Co., Sept. 10, 1914, *2533*.

*Leptaxis Menziesii* (Pursh) Raf.—Hood River, July 24, 1915, *3318*, *3359*.

*Mitella Breweri* Gray?—N. slope Mt. Jefferson, Aug. 27, 1916, H. P. Barss, *3397*.

*Mitella ovalis* Greene—Mary's Peak, Benton Co., May 23, 1915, *3037*.

*Mitella* sp.—N. slope Mt. Jefferson, 8,000 ft., Aug. 8, 1914, H. P. Barss & G. B. Posey, *2529*.

*Tellima grandiflora* (Pursh) Dougl.—Corvallis, July 15, 1910, *1122*, Apr. 8, 1914, *3075;* Austin, Grant Co., Aug. 1915, J. R. Weir, *214*.

*Tiarella unifoliata* Hook.—Bridal Veil, Multnomah Co., Aug. 11, 1910, *1070;* Ashland, Jackson Co., Sept. 10, 1914, *3028*.

115. **Puccinia hieraciata** (Schw.) comb. nov.

*Caeoma* (*Aecidium*) *hieraciatum* Schw. Trans. Am. Phil. Soc. II. 4: 292. 1832.

*Puccinia patruelis* Arth. Mycol. 1: 245. 1909.

On Cyperaceae: II, III.

*Carex praegracilis* Boott (*C. marcida* Boott)—Ontario, Malheur Co., Aug. 1901, Griffiths & Morris; Andrews, Harney Co., Aug. 1901, Griffiths & Morris (Griffiths, W. Am. Fungi *339a*).

This species shows a distribution from coast to coast and has aecia on Cichoriaceous hosts. Arthur (l. c.) has conducted one successful culture and obtained the development of pycnia and aecia on *Agoseris glauca* following sowings of teliosporic material on *Carex pratensis* from Colorado. Other aecia having a similar morphology, including a rare form on *Hieracium* collected by Schweinitz, on which the present name is based, are properly referred here. No aecial collections have been made in Oregon.

116. Puccinia Hieracii (Schum.) Mart. Fl. Mosq. 226. 1812.

*Uredo Hieracii* Schum. Enum. Pl. Saell. 2: 232. 1803.

*Puccinia sejuncta* Syd. Ann. Myc. 1: 236. 1903.

On Cichoriaceae:

*Hieracium albiflorum* Hook.—Hood River, May 16, 1915, *3312*, July 23, 1915, *3311*.

*Hieracium cinereum* Howell—Hood River, July 22, 1915, *3324*.

*Hieracium gracile* Hook.—N. slope Mt. Jefferson, Aug. 6, 1914, H. P. Barss, *2541*.

*Hieracium scouleri* Hook.—Austin, Grant Co., Aug. 1915, J. R. Weir, *156*.

*Hieracium* sp.—Hilgard, Union Co., July 9, 1914, *3319;* Austin, Grant Co., Aug. 1915, J. R. Weir, *213;* Klamath Falls, Klamath Co., Sept. 3, 1906, J. R. Weir, *240*.

This species may occur on the same plants with *Aecidium columbiense* (cf. 215) which is doubtless the aecial stage of some heteroecious rust not yet determined. Sydow (l. c.) has described *P. sejuncta* based on such a mixture.

117. Puccinia Holboellii (Hornem.) Rostr. Middelser om Groenland 3: 534. 1888.

*Aecidium Holboellii* Hornem. Fl. Dan. 37: 11. 1840.

*Puccinia Barbareae* Cooke, Grevillea 8: 34. 1879.

The type of *P. Barbareae* was described as on a "Cruciferous plant" from Oregon, Dr. Lyall *61*. The data on the type collection at the Kew Herbarium reads "Oregon Boundary Commission, Ft. Coville to Rocky Mts. 1861, Dr. Lyall *61*." Since Ft. Coville is in northeastern Washington there would seem to be little chance of this collection having been made within the state of Oregon. However, since it has been recorded from our limits both in the original description and by Holway (N. Am. Ured. 1: 45. 1906) it is included here with the above explanation. The species undoubtedly does occur in eastern Oregon as the range includes all the surrounding states.

118. Puccinia holcina Erikss. Ann. Sci. Nat. 9: 274. 1899.

On Poaceae:

*Holcus lanatus* L.—Corvallis, June 10, 1915, *2678*, June 12, 1915, *3113;* Toledo, Lincoln Co., July 19, 1915, *3116;* Yaquina, Lincoln Co., July 17, 1915, *3117;* Salem, Marion Co., May 1, 1914, G. H. Godfrey, *3118;* Portland, Aug. 19, 1915, E. Bartholomew (Barth. Fungi Columb. *4852*).

Evidently a common rust in western Oregon, otherwise known from North America from a few other collections made on the Pacific coast from California to Vancouver Island, B. C., and from a single locality along the eastern coast in Massachusetts. This species may be easily separated from *P. Rhamni* (cf. 159) in the telial stage by the evenly thickened apices of the teliospores. The urediniospores of the two rusts are similar. Those of the present species are somewhat larger and globoid, 19–24 by 23–27 $\mu$, while in *P. Rhamni* they are globoid or broadly ellipsoid, 16–20 by 18–24 $\mu$.

The aecial connection is unknown. The rust has evidently been introduced from Europe and is able to maintain itself by over-wintering urediniospores.

119. Puccinia Hypochoeridis Oud. Nederl. Kruidk. Arch. II, 1: 175. 1872.

On Carduaceae:

*Hypochaeris radicata* L.—Myrtle Creek, Douglass Co., June 9, 1914, F. D. Bailey, *2543*.

120. **Puccinia insperata** sp. nov.

O. Pycnia not seen.

I. Aecia chiefly hypophyllous and petiolicolous; in crowded groups on yellowish spots 2–3 mm. across; cupulate, 0.2–.25 mm. broad; peridium whitish, margin recurved, lacerate; peridial cells rhombic, 19–27 by 35–45 $\mu$, overlapping, outer wall 1–1.5 $\mu$ thick, inner wall 3–4 $\mu$ thick, verrucose; aeciospores globoid or broadly ellipsoid, 15–19 by 19–23 $\mu$, wall colorless, 1–1.5 $\mu$ thick, finely and closely verrucose.

II. Uredinia amphigenous, scattered, round, 0.2–0.5 mm. across, tardily naked, pulverulent, pulvinate, cinnamon brown, ruptured epidermis conspicuous; urediniospores subglobose or broadly ellipsoid, occasionally obovate, 19–21 by 23–29 $\mu$; wall cinnamon brown, 1.5–2 $\mu$ thick, minutely and closely echinulate, pores 2–3, scattered.

III. Telia amphigenous and petiolicolous, scattered, round, 0.2–0.8 mm. across, tardily naked, pulvinate, becoming pulverulent, blackish brown, ruptured epidermis conspicuous; teliospores ellipsoid or broadly obovoid, occasionally somewhat irregular, 16–20 by 23–32 $\mu$, rounded at both ends, scarcely or not at all constricted, wall chestnut brown, 1.5–2 $\mu$ thick, uniform, smooth; pedicel colorless, deciduous.

On Cichoriaceae:

*Nabalus hastatus* (Less) Heller—Hood River, May 16, 1915, *2662*, July 24, 1915, *3265*, type.

A very distinct species separable from the eastern *P. orbicula* Pk. by the smooth teliospores and the presence of a definite peridium in the aecidium. The two collections were made at the same spot. The first shows aecia unaccompanied by pycnia, associated with telia chiefly on the petioles, suggesting strongly an opsis-form. The second collection, however, shows scattered uredinia and telia with a few old aecia.

121. Puccinia Iridis (DC.) Wallr. in Rabenh. Krypt. Fl. 1: 23. 1844.

*Uredo Iridis* DC. Encycl. 8: 224. 1808.

On Iridaceae:

*Iris tenax* Dougl.—Corvallis, June 24, 1914, F. D. Bailey, *1343;* Wren, Benton Co., July 22, 1914, *1413*, Ashland, Jackson Co., Sept. 10, 1914, *1994*.

122. Puccinia Jonesii Pk. Bot. Gaz. 6: 226. 1881.

*Allodus Jonesii* Arth. Résult Sci. Congr. Bot. Vienne 345. 1906.

On Umbelliferae:

*Peucedanum triternata* (Pursh) Nutt.—Austin, Grant Co., Aug. 1915, J. R. Weir, *149*, *151*.

123. Puccinia Ligustici Ell. & Ev. Bull. Torrey Club **22**: 263. 1895.
*Puccinia luteobasis* Ell. & Ev. Bull. Torrey Club **24**: 457. 1897.
On Umbelliferae:
*Ligusticum apiifolium* (Nutt.) Gray—Corvallis, 1911, *1166*, April 15, 1913, F. D. Bailey, *3080*, March 23, 1914, G. B. Posey, *3328*, March 22, 1914, G. H. Godfrey, *2549;* Orenco, Washington Co., June 23, 1913, *3079*.

124. Puccinia luxuriosa Sydow, Monog. Ured. **1**: 812. 1904.
*Puccinia tosta luxurians* Arth. Bull. Torrey Club **29**: 229. 1902.
On Poaceae:
*Sporobolus airoides* Torr.—Andrews, Harney Co., Aug. 1901, Griffiths & Morris (Griffiths, W. Am. Fungi *304*).

Bethel (Phytopath. **7**: 93. 1917) has reported successful cultures of this rust on *Sarcobatus vermiculatus*, amply supported by field observations. Arthur (Mycol. **1**: 234. 1909) has infected that host with teliospores of *P. subnitens* (cf. 167) from Nevada. Bethel, however, failed to obtain infection on any of the aecial hosts for that species with teliospores from *Sporobolus airoides* in Colorado. It is possible that the two forms represent biological races of the same species and should be united.

125. Puccinia Majanthae (Schum.) Arth. & Holw. Bull. Lab. Nat. Hist. Univ. Iowa **5**: 188. 1901.
*Aecidium Majanthae* Schum. Enum. Pl. Saell. **2**: 224. 1803.
*Puccinia sessilis* Schneider, in Schröter Abh. Schles. Ges. **49**: 19. 1870.
On Poaceae:
*Phalaris arundinacea* L.—Beulah, Malheur Co., Aug. 1901, Griffiths & Morris (Griffiths, W. Am. Fungi *26a*).

No culture work has been reported in America. In Europe the aecia have been found on *Allium*, *Arum*, *Convallaria* and various other related hosts. Various names have been given to the different biological forms (Klebahn, Die Wirtsw. Rostp. 263–272. 1904; Sydow, Monog. Ured. **1**: 776–784. 1904). Aecia on *Smilacina*, *Polygonatum*, *Maianthemum* and *Uvularia* from the central and eastern United States doubtless belong here in whole or in part.

126. Puccinia Malvacearum Bert. Gay's Hist. de Chile **8**: 43. 1852.
On Malvaceae:
*Abutilon* ? sp. (cultivated shrub)—Corvallis, May, 1914, W. E. Lawrence, *3364*, Nov. 17, 1914, W. E. Lawrence, *3363*, Jan. 12, 1915, *2627*.

*Althaea ficifolia* Cav.—The Dalles, Wasco Co., Aug. 25, 1915, E. Bartholomew (Barth. Fungi Columb. *4758*, N. Am. Ured. *1559*).

*Althaea rosea* Cav.—Corvallis, April 27, 1907, E. R. Lake, *1299*, Aug. 1909, *1068*, Sept. 1910, *1014*, Jan. 12, 1915, W. E. Lawrence, *2627;* Gibbon, Umatilla Co., June 5, 1911, comm. *1850;* Klamath Falls, Klamath Co., Sept. 19, 1911, *1031;* Salem, Marion Co., May 2, 1913, comm. *1866;* Svenson, Clatsop Co., June 5, 1913, comm. *1895;* Grant's Pass, Josephine Co., July, 1913, *1926;* Dayton, Yamhill Co., April 6, 1914, comm. *1479;* Lents, Clackamas Co., April 27, 1914, comm. *1936;* Ione, Morrow Co., June 26, 1914, comm. *1937;* The Dalles, Wasco Co., July 1, 1914, *1342;* Hillsboro, Washington Co., July 26, 1914, *1738;* Medford, Jackson Co., March 31, 1915, *2556.*

*Malva rotundifolia* L.—Corvallis, Apr. 12, 1909, J. C. Bridwell, *3388*, Aug. 30, 1913, *1141*, Feb. 14, 1914, *1181;* The Dalles, Wasco Co., July 1, 1914, *1303.*

*Malva ?* sp.—New Pine Creek, Lake Co., July, 1910, comm. *3376.*

127. Puccinia McClatchieana Diet. & Holw. Erythea 2: 127. 1894.

On Cyperaceae:

*Scirpus microcarpus* Presl.—Elgin, Union Co., Aug. 19, 1897, E. P. Sheldon, *8735;* Beulah, Malheur Co., Aug. 1901, Griffiths & Morris (Griffiths, W. Am. Fungi *348*); Glenbrook, Benton Co., Aug. 1909, *1190;* Hubbard, Marion Co., May 27, 1914, *2518;* Gresham, Multnomah Co., June 6, 1914, F. D. Bailey, *2516;* Tualatin, Washington Co., July 10, 1914, F. D. Bailey, *1356;* Hood River, Aug. 5, 1914, *2520;* Mary's Peak, Benton Co., Aug. 15, 1914, *2517;* Orenco, Washington Co., April 2, 1915, *3386;* Yaquina, Lincoln Co., July 20, 1915, *3317;* Toledo, Lincoln Co., July 19, 1914, *3012.*

128. Puccinia melanconoides Ell. & Hark. Bull. Calif. Acad. Sci. 1: 27. 1884.

*Allodus melanconioides* Arth. Result Sci. Congr. Bot. Vienne 345. 1906.

On Primulaceae:

*Dodecatheon latifolium* (Hook.) Piper—Hills, N. W. Corvallis, April 5, 1914, *1290*, May 1, 1915, *3049*, April 13, 1912, F. D. Bailey, *1001;* Moist Woods (Corvallis?), April, 1897, Moses Craig.

129. Puccinia Menthae Pers. Syn. Fungi 227. 1801.

On Labiatae:

*Mentha canadensis* L.—Corvallis, Aug. 10, 1910, *1167*, Nov. 4, 1911, *1172;* Clatskanie, Columbia Co., Oct. 6, 1914, F. D. Bailey, *3099;* Portland, Aug. 21, 1915, E. Bartholomew (Barth. Fungi Columb. *4968*).

*Mentha canadensis lanata* Piper—Toledo, Lincoln Co., Sept 25, 1911, F. D. Bailey, *1162.*

*Mentha piperata* L.—Grant's Pass, Josephine Co., Sept. 3, 1916, J. R. Weir, *255*.

*Mentha spicata* L.—Hood River, Aug. 6, 1914, *1482;* Elk City, Lincoln Co., Aug. 20, 1914, *3217;* Portland, April, 1914, comm. *3208;* The Dalles, Wasco Co., July 1, 1914, *1340*.

130. Puccinia mesomegala B. & C. in Peck, Rep. N. Y. State Mus. 25: 111. 1873.

*Dicaeoma mesomegalum* Kuntze, Rev. Gen. Pl. 3: 469. 1898.

On Convallariaceae:

*Clintonia uniflora* Kunth.—Mt. Hood, Sept. 1, 1901, E. W. D. Holway, *1016*, Road to Mt. Hood, Aug. 7, 1914, *1601;* Klamath Co., Oct. 7, 1903, E. B. Copeland (Sydow, Ured. *1776*); Bridal Veil, Multnomah Co., Aug. 11, 1910, *1079;* Parkdale, Hood River Co., March 20, 1915, L. Childs, *3188;* Sumpter, Baker Co., July 16, 1913, J. R. Weir, *216*.

This very distinct micro-form is very common in the mountains of the northwestern states on the above host, and on *C. borealis* in the northern tier of states from New Hampshire to Minnesota and in Canada.

131. Puccinia micromeriae Dudley & Thomp. Jour. Myc. 10: 54. 1904.

On Labiatae:

*Micromeria chamissonis* (Benth.) Greene (*M. Douglasii* Benth.)—Mary's Peak, Benton Co., June 20, 1910, *3163;* Corvallis, June, 1910, *1157*, May 4, 1912, F. D. Bailey, *1134;* Philomath, April 20, 1912, F. D. Bailey, *1136*, Jan. 6, 1914, *1154;* Eugene, Lane Co., July 11, 1914, G. B. Posey, *1292;* N. slope Mt. Hood, Aug. 7, 1914, *2560;* Washington Co., July–Aug. 1897, Moses Craig; Grant's Pass, Josephine Co., Sept. 3, 1916, J. R. Weir, *252*.

132. Puccinia microsora Körn.; Fuckel, Fungi Rhenani 2637. 1874.

On Cyperaceae:

*Carex mirata* Dem.—Clatsop, Clatsop Co., Nov. 7, 1913, *1196*.

Otherwise known only locally from the eastern United States. The aecial stage is unknown.

133. Puccinia Millefolii Fckl. Sym. Myc. 55. 1869.

On Carduaceae:

*Achillea millefolium* L.—Philomath, May 10, 1914, *1834;* Yaquina River, Elk City, Lincoln Co., Aug. 20, 1914, *1625;* Hood River, July 22, 1915, *3139*.

This micro-form, evidently introduced from Europe, is otherwise

known only from a few collections made in California and single collections from Montana and New Mexico.

134. PUCCINIA MONARDELLAE Dudley & Thomp., Jour. Myc. 10: 53. 1904.

ON LABIATAE:

*Monardella odoratissima* (Benth.) Greene—Hilgard, Union Co., July 10, 1914, *1531*.

*Monardella villosa* Benth.—Ashland, Jackson Co., Sept. 10, 1914, *2542;* Myrtle Creek, Douglass Co., June 9, 1914, F. D. Bailey, *2534*.

135. PUCCINIA MONOICA (Pk.) Arth. Mycologia 4: 61. 1912.

*Aecidium monoicum* Peck, Bot. Gaz. 4: 230. 1879.

ON POACEAE: III.

*Koeleria cristata* (L.) Pers.—Austin, Grant Co., Aug. 1915, J. R. Weir, *237*.

This species has aecia on *Arabis* as has been shown by Arthur (Mycol. 4: 59. 1912; 7: 75. 1915). No aecial collections have been seen from Oregon but this stage undoubtedly occurs in the eastern part of the state. The collection cited under *P. Holboellii* (cf. 117) was said to have aecia on a part of the original specimen which undoubtedly are to be referred here rather than to *A. Barbareae* DC. as was done by Vize in the original notice of *P. Barbareae*.

136. PUCCINIA MONTANENSIS Ellis, Jour. Myc. 7: 274. 1883.

*Aecidium Hydrophylli* Pk. Bull. Buff. Soc. 1: 68. 1873.

*Aecidium Phaceliae* Pk. Bull. Torrey Club 11: 50. 1884.

*Aecidium Mertensiae* Arth. Bull. Torrey Club 31: 6. 1904.

ON HYDROPHYLLACEAE: I.

*Hydrophyllum albifrons* Heller—Corvallis, April 5, 1914, *1289;* Mary's Peak, Benton Co., May 21, 1915, *3029*.

*Hydrophyllum capitatum* Dougl.—Near Crystal Lake, Corvallis, May 20, 1899, E. R. Lake, *1600*.

*Hydrophyllum tenuipes* Heller—Corvallis, April, 1910, *1111, 3105;* April 15, 1912, F. D. Bailey, *1124*.

*Hydrophyllum* sp.—Horse Creek Cañon, Wallowa Co., May 14, 1897, E. P. Sheldon, *8040*.

*Mertensia laevigata* Piper—Jefferson Lake, Marion Co., Aug. 1892, Moses Craig; Parmelia Lake, Cascade Mts., July 2, 1914, J. H. Corsaut, *2554*.

ON BORAGINACEAE: I.

*Phacelia heterophylla* Pursh—Philomath, April 20, 1912, *1168*.

*Phacelia leucophylla* Torr.—Austin, Grant Co., Aug. 1915, J. R. Weir, *155*.

On Poaceae: II, III.

*Elymus glaucus* Buckl.—Glendale, Douglass Co., July 17, 1914, *1347*.

The aecial stage of this rust is very common in western Oregon particularly on *Hydrophyllum*. The uredinial and telial stages are doubtless much more common than the single record above would indicate. The species is very difficult to separate in the uredinial stage from *P. Clematidis* (cf. 85) and it is probable that some of the collections referred to that species belong here.

Arthur (Mycol. 8: 139. 1916) sowed aecia from *Hydrophyllum capitatum* on *Agropyron tenerum* and *Elymus virginicus*. On the former uredinia and telia developed, and on the latter a few uredinia only. This is the only successful culture with this species, though aecia on other Hydrophyllaceae and on Boraginaceae are referred here on morphological grounds.

137. Puccinia mutabilis Ellis & Gal. Jour. Myc. 5: 67. 1889.

On Alliaceae:

*Allium Geyeri* Wats.—Blue Mts., July 5, 1897, W. C. Cusick, *1827*.

The writer is indebted to Professor Holway for the specimen on which this record is based.

138. Puccinia madiae Syd. Monog. Ured. 1: 121. 1902.

On Carduaceae:

*Madia elegans* Don.—Corvallis, June, 1910, *2619*.

*Madia glomerata* Hook.—Corvallis, Aug. 1899, E. R. Lake.

*Madia* sp.—Hood River, June 20, 1914, *3349*.

This species is very close to, and possibly identical with, *P. Hemizoniae* (cf. 113).

139. Puccinia obscura Schroet., Pass. Nuov. Giorn. Bot. Ital. I, 9: 256. 1877.

*Aecidium Bellidis* Thüm. Fungi Austr. 635. hyponym. 1873.

*Puccinia Bellidis* Lagerh. Bol. Soc. Broter. 8: 134. 1890.

On Juncaceae:

*Juncoides parviflorum* (Ehrh.) Coville—Ashland, Jackson Co., Sept. 10, 1914, *2519;* Bend, Crook Co., Sept. 11, 1916, J. R. Weir, *200;* Ukiah, Umatilla Co., Aug. 21, 1903, M. A. Crosby.

No culture work has been conducted in America. Plowright (Jour. Linn. Soc. Lond. 20: 511. 1884) has shown the aecia to be *A. Bellidis*, having cultured the species in both directions. Other European workers have confirmed Plowright's results (Klebahn, Die Wirtsw. Rostp. 317. 1904).

140. Puccinia obtecta Pk. Bull. Buff. Soc. Nat. Hist. 1: 66. 1873.
*Aecidium compositarum Bidentis* Burrill; DeToni in Sacc. Syll. Fung. 7: 799. 1888.

On Cyperaceae:

*Scirpus americanus* Pers. (*S. pungens* Vahl.)—Westfall, Malheur Co., Aug. 1901, Griffiths & Carter (Griffiths, W. Am. Fungi *353*).

Arthur (Jour. Myc. 14: 20. 1908) has cultured this species on *Bidens*. Using telia on *S. americanus* from Indiana successful infection resulting in pycnia and aecia was obtained on *B. frondosa* and *B. connata*. Aecia have not been collected west of the Rocky Mt. region. The above collection was issued as *P. canaliculata*, which is now interpreted as occurring only on *Cyperus* having aecia on *Xanthium* and is unknown in Oregon.

141. **Puccinia Ortonii** sp. nov.

O. Pycnia few, imperfectly known.

I. Aecia chiefly hypophyllous, gregarious, in roundish or elongated groups 6–8 mm. across, short cupulate, 0.2–0.3 mm. in diameter; peridium yellowish, the margin erose; peridial cells oblong or rhombic, 20–26 by 29–35 μ, slightly overlapping, the outer wall finely striate, 8–10 μ thick, the inner verrucose or slightly tuberculate, 4–6 μ thick; aeciospores globoid or broadly ellipsoid, 18–19 by 19–24 μ, wall colorless, 1–1.5 μ thick, very closely and finely verrucose.

II. Uredinia amphigenous, scattered, round, 0.5–1 mm. across, tardily naked, cinnamon brown, cinereous when covered, ruptured epidermis conspicuous, pulverulent; urediniospores broadly ellipsoid (or when young obovoid), 19–26 by 23–32 μ, wall cinnamon brown, 2–3 μ thick, moderately and very minutely and obscurely echinulate; pores 3–5, scattered.

III. Telia amphigenous, scattered, round, 0.2–1 mm. across, tardily naked, ruptured epidermis conspicuous, chestnut brown, cinereous when covered, pulvinate, somewhat pulverulent; teliospores broadly and somewhat angularly ellipsoid, 18–26 by 30–42 μ, rounded at both ends, slightly or not constricted at the septum, wall chestnut brown, 1.5–2.5 μ thick, uniform, smooth, with hyaline papilla over pore of apical cell which is usually at the apex but occasionally placed laterally, pore of lower cell varying in position from near the pedicel to the septum; pedicel deciduous, colorless.

On Primulaceae:

*Dodecatheon Hendersonii leptophylla* Suks.—Lake of the Woods, Cascade Range, Aug. 1892, Moses Craig.

The above collection bears aecia and uredinia only. This species differs from *P. melancoides* (cf. 128) in the presence of uredinia in the life cycle. It is to be regarded as a correlated form with that species.

The species is dedicated to Prof. C. R. Orton who was the first to separate the material from the opsis-form. The following is a list of the specimens from other localities in the Arthur herbarium.

*Dodecatheon alpinum* Greene—Susanville, California, 5,000 ft., June 30, 1897, II, iii, M. E. Jones; Bluff Lake, San Bernardino Mts., California, 7,400 ft., Sept. 1895, III, Miss Nora Pettibone, *2853;* Mt. Eddy, Siskiyou Co., California, Sept. 7, 1903, i, ii, III, E. B. Copeland, (Sydow, Ured. *1774,* type).

*Dodecatheon Jeffreyi* Van Houtte—South of Sitka, Alaska, ii, III, Aug. 29, 1916, J. P. Anderson, *337;* Vancouver Island, British Columbia, Aug. 26, 1908, ii, III, E. W. D. Holway.

*Dodecatheon* (*tetrandrum* Suks.?)—Mt. Adams, Washington, 6,000–7,000 ft., Aug. 31, 1886, W. N. Suksdorf (Barth. N. Am. Ured. *554, 1457*).

142. Puccinia Oxyriae Fckl. Symb. Nachtr. 3: 14. 1875.

On Polygonaceae:

*Oxyria digyna* (L.) Hill—Strawberry Mt., 8,000 ft., Grant Co., Sept. 2, 1913, W. E. Lawrence, *1112.*

Evidently a rather rare species represented in the Arthur herbarium otherwise only by single collections from Colorado, Utah, Idaho, Alberta and British Columbia on the above host.

143. Puccinia Palmeri D. & H. Erythea 7: 98. 1899. (Not *Aecidium Palmeri* And. 1891.)

*Allodus Palmeri* Orton, Mem. N. Y. Bot. Gard. 6: 202. 1916. (Not *A. Palmeri* Arth. 1906.)

On Scrophulariaceae:

*Pentstemon Menziesii* Hook.—Near Mt. Jefferson, Linn Co., July 3, 1914, F. D. Bailey, *3046;* Mt. Hood, 6,000 ft., Sept. 1, 1901, E. W. D. Holway; Horse Creek, Wallowa Co., June 24, 1897, E. P. Sheldon, *8368.*

This is an opsis-form common in the Rocky Mt. and north Pacific states. Dietel & Holway (l. c.) based their combination on *Aecidium Palmeri* Anderson. This *Aecidium,* as has been recently determined by Orton, working in this laboratory, is the aecial stage of the heteroecious rust *P. Andropogonis* Schw. and not the aecia of this species. While the name *P. Palmeri* D. & H. has been misapplied in this way it seems best to retain it for this species, particularly since the telia described apply to this fungus.

144. Puccinia Parkerae Diet. & Holw. Erythea 3: 78. 1895.

On Saxifragaceae:

*Ribes lacustre* (Pers.) Poir.—Whitewater Ranger Station, near Mt. Jefferson, Aug. 28, 1916, H. P. Barss, *3398;* Hood River, July 23, 1915, *3016.*

This short-cycled form possesses teliospores which closely resemble the telia of the *Carex* rusts having aecia on *Ribes* (cf. *P. Grossulariae*, 109) as has been pointed out by Holway (N. Am. Ured. 1: 53. 1906). It is not to be confused with the rust having a similar life history in the eastern United States, *P. Ribis* DC. The latter has verrucose spores, while in the one under discussion the spores are smooth.

145. Puccinia Pattersoniana Arth. Bull. Torrey Club 33: 29. 1906.
On Poaceae:

*Agropyron spicatum* (Pursh) Rydb.—Dufur, Wasco Co., June 19, 1914, *1398;* Hilgard, Union Co., July 10, 1914, *1364;* Grant's Pass, Josephine Co., Sept. 3, 1916, J. R. Weir, *208.*

The aecial form of this distinct heteroecious rust is unknown.

146. Puccinia Peckii (DeToni) Kellerm. Jour. Myc. 8: 20. 1902.

*Aecidium Oenotherae* Pk. Ann. Rep. N. Y. State Mus. 23: 60. 1873. (Not *P. Oenotherae* Vize, 1877.)

*Aecidium Peckii* DeToni, in Saccardo Syll. Fung. 7: 790. 1888.

? *Puccinia ludibunda* E. & E. Proc. Phil. Acad. 1893: 153. 1893.
On Cyperaceae:

*Carex Hookeriana* Dewey—Springbrook, Yamhill Co., May 14, 1914, F. D. Bailey, *3015;* Whitewater Station near Mt. Jefferson, Aug. 12, 1914, H. P. Barss & G. B. Posey, *3006.*

The above collections are referred somewhat doubtfully to this species as no aecia have been collected in the Pacific northwest.

The aecia occur on Onagraceae as was first shown by Kellerman (l. c.) and later by Arthur (Bot. Gaz. 33: 13. 1903; Jour. Myc. 8: 52. 1902; 11: 58. 1905; 12: 15. 1906; 13: 195. 1907; Mycol. 1: 233. 1909; 2: 222. 1910; 4: 15. 1912).

147. Puccinia Pentastemonis Pk. Bull. Torrey Club 12: 35. 1885.
On Scrophulariaceae:

*Pentstemon diffusus* Dougl.—Bridal Veil, Multnomah Co., May 18, 1915, *3267.*

148. Puccinia Pimpinellae (Str.) Mart. Fl. Mosq. Ed. II: 226. 1817.

*Uredo Pimpinellae* Strauss, Wett. Ann. 2: 102. 1810.

*Puccinia Osmorrhizae* Cke. & Peck, in Peck, Rep. N. Y. State Mus. 29: 73. 1878.

*Puccinia trifoliata* E. & E. Bull. Torrey Club 22: 58. 1895.
On Umbelliferae:

*Osmorrhiza brevipes* (Coulter & Rose) Suks.—Corvallis, May 4, 1912, F. D. Bailey, *2550,* July 3, 1914, G. B. Posey, *1998,* Apr. 28, 1915, *3313;* Grant's Pass, Josephine Co., Sept. 3, 1916, J. R. Weir, *196;* Austin, Grant Co., Aug. 1915, J. R. Weir, *189.*

*Osmorrhiza divaricata* Nutt.—Jackson Co., Sept. 7, 1903, E. B. Copeland (Sydow, Ured. *1778*); Mt. Hood, Hood River Co., Aug. 7, 1914, *3081*.

*Osmorrhiza Liebergii* (Coulter & Rose) Suks.—North of Mt. Jefferson, Aug. 28, 1916, H. P. Barss, *3400*.

*Osmorrhiza occidentalis* Nutt.—Paisley, Lake Co., Aug. 1914, J. C. Elder, *3183*.

149. Puccinia Piperi Ricker, Jour. Myc. **11**: 114. 1905.

On Poaceae: II and III.

*Festuca pacifica* Piper—Eight Dollar Mt., Oregon, June 12, 1904, C. V. Piper, *6502*, type.

This species is evidently rare, since it is known only from the type locality listed above and from two localities in California. The life history is unknown.

150. Puccinia plumbaria Pk. Bot. Gaz. **6**: 238. 1881.

*Aecidium Giliae* Pk. Bot. Gaz. 4: 230. 1879. (Not *P. Giliae* Hark. 1884.)

*Allodus Giliae* Orton, Mem. N. Y. Bot. Gard. **6**: 199. 1916.

On Polemoniaceae:

*Gilia gracilis* (Dougl.) Hook.—Mary's Peak, Benton Co., May 21, 1915, *3310;* Hood River, May 14, 1914, *1526*, *2514*, June 9, 1915, *3274*.

*Phlox speciosa* Pursh—Sherman, Sherman Co., July 1, 1914, *2515*.

151. Puccinia poculiformis (Jacq.) Wettst. Verhl. Zool. Bot. Ges. Wein **35**: 544. 1885.

*Lycoperdon poculiforme* Jacq. Coll. Austr. **1**: 122. 1786.

*Aecidium Berberidis* Pers. in Gmel. Syst. Nat. **2**: 1473. 1791.

*Puccinia graminis* Pers. Neues Mag. Bot. **1**: 119. 1794.

*Puccinia Phlei-pratensis* Erikss. & Henn. Zeit. f. Pflanzenkr. 4: 140. 1894.

*Uredo quinqueporula* Arth. & Fromme, Torreya **15**: 265. 1915.

On Poaceae: II, III.

*Agropyron dasystachyum* (Hook.) Vasey—Sherman Sta. O. W. R. R. & Nav. Co., Sherman Co., July 1, 1914, *1420*.

*Agrostis exarata* Trin.—Ashland, Jackson Co., Sept. 10, 1914, *1567*.

*Alopecuris californicus* Vasey—Corvallis, Sept. 21, 1914, *1552*.

*Avena fatua glabrata* Peterm.—Philomath, Jan. 16, 1914, *1138*.

*Avena sativa* L.—Corvallis, Aug. 12, 1911, *3161*, July 6, 1914, *1667*, Aug. 13, 1914, *1661*, Aug. 9, 1915, G. H. Godfrey & F. D. Bailey, *3135;* Cottage Grove, Lane Co., July 14, 1914, *1674;* Pleasant Hill, Lane Co., Aug. 7, 1913, F. D. Bailey, *1130*.

*Beckmannia erucaeformis* (L.) Host.—Corvallis, Aug. 8, 1915, *3026a*.

*Dactylis glomerata* L.—Cottage Grove, Lane Co., July 14, 1914, *1670;* Corvallis, July 6, 1914, *1666;* Clatsop, Clatsop Co., Nov. 3, 1913, *1155;* Philomath, Jan. 6, 1914, *1084*.

*Deschampsia elongata* (Hook.) Munro—Glendale, Douglass Co., July 17, 1914, *1410;* Ashland, Jackson Co., Sept. 10, 1914, *1566, 1568;* Wren, Benton Co., June 26, 1914, *1329;* Garden Home, Multnomah Co., July 20, 1915, *3157, 3158*.

*Elymus glaucus* Buckl.—Philomath, Jan. 1, 1914, *1152;* Bend, Crook Co., Sept. 11, 1916, J. R. Weir, *211*.

*Festuca elatior* L.—Wren, Benton Co., June 26, 1914, *1324;* Cottage Grove, Lane Co., July 14, 1914, *1348;* Corvallis, July 29, 1915, *3190*.

*Festuca megalura* Nutt.—Corvallis, June 24, 1914, *1390*, Aug. 13, 1914, *3191*.

*Festuca myuras* L.—Cottage Grove, Lane Co., July 14, 1914, *1351*.

*Festuca pacifica* Piper—Corvallis, July 6, 1914, *1434*, July 29, 1914, *1416*.

*Hierochloe macrophylla* Thurb.—Glendale, Douglass Co., July 17, 1914, *1411* (type of *Uredo quinqueporula*).

*Hordeum distichon* L.—Corvallis, Aug. 20, 1915, H. P. Barss, *3184*.

*Hordeum vulgare* L.—Corvallis, Oct. 5, 1914, *3165*.

*Lolium multiflorum* Lam.—Cottage Grove, Lane Co., July 14, 1914, *1349;* Corvallis, Sept. 20, 1914, *1551;* Tualatin, Washington Co., July 10, 1914, F. D. Bailey, *1357*.

*Lolium subulatum* Vis.—Corvallis, March 22, 1915, *3277*.

*Phleum pratense* L.—Cottage Grove, Lane Co., July 14, 1914, *1668;* Hood River, June 19, 1914, *1665;* Springbrook, Yamhill Co., June 22, 1914, F. D. Bailey, *3136;* Briton, Lincoln Co., July 17, 1915, VanGundia, *3086, 3087;* Corvallis, Aug. 13, 1914, *1662;* Philomath, Jan. 1, 1914, *1151;* Gresham, Multnomah Co., Aug. 7, 1913, F. D. Bailey, *1140;* Sumpter, Baker Co., June, 1913, J. R. Weir, *97;* Grant's Pass, Josephine Co., Sept. 2, 1916, J. R. Weir, *246*.

*Triticum compactum* Host.—Moro, Sherman Co., June 11, 1915, F. K. Ravn & A. G. Johnson.

*Triticum vulgare* L.—Corvallis, July 29, 1914, *1684;* Hood River, Aug. 5, 1914, *1669;* Ashland, Jackson Co., Aug. 28, 1913, *1125;* Union, Union Co., Aug. 13, 1915, F. D. Bailey, *3133;* Albany, Linn Co., Aug. 22, 1900, E. B. Townsend, *3384*.

Since the classic researches of DeBary, who first demonstrated heteroecism in rusts by showing that this species has aecia on *Berberis*, this rust has received more attention on the part of investigators than any other species. (Klebahn, Die Wirtsw. Rostp. 205–235. 1904.)

In America the most important work has been conducted by Carleton (Div. Veg. Phys. & Path. U. S. D. A. Bull. 16. 1899; Bur. Pl. Industry, U. S. D. A. Bull. 63. 1904); Arthur (Jour. Myc. 8: 53. 1902; 11: 57. 1905; 12: 17. 1906; 13: 198. 1907; 14: 16. 1908; Mycol. 2: 227. 1910; 4: 18. 1912); Freeman & Johnson (Bur. Pl. Ind. U. S. D. A. Bull. 216. 1911); Stakman (Minn. Exp. Sta. Bull. 138. 1914; Jour. Agr. Research 4: 193–199. 1915) and Stakman and Piemeisel (Jour. Agr. Research 6: 813–816. 1916; 10: 429–495. 1917).

In Oregon the rust is apparently not as important on wheat and other grains as it is in the spring wheat districts east of the Rocky mountains. No aecial collections have been made.

A number of unrecorded hosts appear in the above list. Since the publication of *Uredo quinqueporula* by Arthur and Fromme (l. c.), telia have been found on a duplicate specimen which determines that that species is properly referred here. The number of pores in the uredospores of that collection is unusual for this rust, the usual number being 4, and in the absence of telia was considered of sufficient importance to separate it as a distinct species.

152. Puccinia Polygoni-alpini Cruchet & Mayor, Bull. Herb. Bois 8: 245. 1908.

On Polygonaceae:

*Rumex paucifolius* Nutt.—Crater Lake, Klamath Co., Sept. 9, 1916, J. R. Weir, *253*.

This specimen is referred to the above species on account of the hyaline umbo covering the pore of the apical cell in the teliospore. The species is described from material on *Polygonum alpinum* from Europe with which our material closely agrees. A collection on that host from Idaho is also to be referred here. The rust is unlike any other recorded on *Rumex*. The only other collection recorded on this host from North America is the one on which *P. uniformis* Pammel & Hume from Wyoming was based, which Holway (N. Am. Ured. 1: 36. 1906) considers to be on *Polygonum* sp. and refers to *P. Bistortae*.

153. Puccinia Polygoni-amphibii Pers. Syn. Fung. 227. 1801.

*Aecidium Geranii maculati* Schw. Schr. Nat. Ges. Leipzig 1: 67. 1822.

On Polygonaceae:

*Polygonum amphibium* L.—Brandt's Ranch, Wallowa Valley, Aug. 26, 1897, E. P. Sheldon, *8972;* The Dalles, Wasco Co., Aug. 25, 1915, E. Bartholomew (Barth. N. Am. Ured. *1566*).

*Polygonum Muhlenbergii* S. Wats. (*P. emersum* Britt.)—The Dalles, Wasco Co., Aug. 26, 1915, E. Bartholomew (Barth. Fungi Columb.

*4762*); Portland, Aug. 21, 1915, E. Bartholomew (Barth. Fungi Columb. *4861*).

*Polygonum pennsylvanicum* L.—Corvallis, Sept. 20, 1914, *1547;* Clatskanie, Columbia Co., Oct. 10, 1914, F. D. Bailey, *1944*.

No collections of aecia referable to this species have been made west of the Rocky mountains. Tranzschel (Centr. f. Bakt. II, 11: 106. 1903) was the first to show that this species has aecia on *Geranium*. Arthur working with American material has confirmed Tranzschel's results (Jour. Myc. 11: 59. 1905; 12: 18. 1906).

154. Puccinia porphyrogenita Curt.; DeToni in Sacc. Syll. 7: 703. 1888.

*Puccinia porphyrogenita* Curt. in Thüm. Myc. Univ. 545 (hyponym). 1876.

*Puccinia acuminata* Pk. Rep. N. Y. State Mus. 23: 57. 1872. (Not *P. acuminata* Fckl. 1869.)

On Cornaceae:

*Cornus canadensis* L.—Near Mt. Jefferson, Aug. 1892, Moses Craig; Larch Mt., Multnomah Co., Aug. 11, 1910, *1078;* South Mt. Jefferson, Linn Co., July 3, 1914, F. D. Bailey, *1840;* Mt. Hood, Aug. 7, 1914, *1604;* Trail to Hanging Valley, Mt. Jefferson, Aug. 11, 1914, H. P. Barss & G. B. Posey, *1622*.

155. Puccinia procera Diet. & Holw. Erythea 1: 249. 1893.

On Poaceae:

*Elymus arenicola* Schrib. & Smith—Umatilla, Umatilla Co., May 11, 1915, *3200*, *3201*, July 11, 1914, *1374*, *1375;* Sherman Sta. O. W. R. R. & Nav. Co., Sherman Co., July 1, 1914, *1421*.

This species is distinguishable from other forms on *Elymus* by the large urediniospores, 26–32 by 32–48 $\mu$. The aecial connection is unknown.

156. Puccinia punctata Link, Ges. Nat. Freunde Berlin Mag. 7: 30. 1816.

On Rubiaceae:

*Galium aparine* L.—Hood River, July 24, 1915, *3225;* Ashland, Jackson Co., Sept. 10, 1914, *3239;* Corvallis, May 1, 1915, *3148*.

*Galium asperrimum* A. Gray—Big Cañon, Wallowa Co., Aug. 24, 1897, E. P. Sheldon, *8774*.

*Galium triflorum* Michx.—Mary's Peak, Benton Co., Aug. 15, 1914, *1513*, *1515;* Elk City, Lincoln Co., Aug. 20, 1914, *2528;* Hood River, July 24, 1915, *3224*.

*Galium* sp.—Philomath, April 20, 1914, F. D. Bailey, *2570;* Corvallis, April 8, 1914, *1524;* Dufur, Wasco Co., June 30, 1914, *1335*.

157. PUCCINIA PYGMAEA Erikss. Fungi Par. Scand. 9: 449. 1895.
ON POACEAE:

*Calamagrostis aleutica* Bong.—Newport, Lincoln Co., July 18, 1915, *3204*, Aug. 30, 1914, *1579*.

The above collections show uredinia only. The aecial connection is unknown.

158. PUCCINIA RECEDENS Syd. Monog. Ured. 1: 146. 1902
ON CARDUACEAE:

*Senecio harfordii* Greenman—Bridal Veil, Multnomah Co., May 18, 1915, *3273*.

*Senecio* sp.—Hilgard, Union Co., July 10, 1914, *1542*.

159. PUCCINIA RHAMNI (Pers.) Wettst. Verhl. Zool.-Bot. Ges. Wein 35: 545. 1885.

*Aecidium Rhamni* Pers. in Gmel. Syst. Nat. 2: 1472. 1791.

*Puccinia coronata* Corda, Icones 1: 6. 1837.
ON RHAMNACEAE: I.

*Rhamnus purshiana* DC.—Corvallis, July 5, 1911, F. D. Bailey, *1135*, May 9, 1914, *1827*, May 12, 1914, *1277*, July 5, 1914, H. P. Barss, *1940;* Hood River, May 14, 1914, *1278;* Clatskanie, Columbia Co., May 20, 1914, F. D. Bailey, *1281;* Cottage Grove, Lane Co., May 1, 1915, C. E. Stewart, *3058*.
ON POACEAE: II, III.

*Agrostis alba* L.—Toledo, Lincoln Co., July 19, 1915, *3119*.

*Agrostis alba maritima* Meyer—Philomath, Jan. 6, 1914, *1149*, *1150*.

*Agrostis exarata* Trin.—Corvallis, Feb. 14, 1914, *3098*, June 29, 1914, G. B. Posey, *1306*, *1308*, Sept. 20, 1914, *1553*, Sept. 5, 1914, *1578*, Dec., 1915, G. B. Posey; Hood River, June 19, 1914, *1401;* Philomath, June 26, 1914, *1344;* Eugene, Lane Co., July 11, 1914, G. B. Posey, *1377;* Newport, Lincoln Co., July 18, 1915, *3120;* Garden Home, Multnomah Co., July 20, 1915, *3121;* Portland, Aug. 21, 1915, E. Bartholomew, *5943*.

*Agrostis foliosa* Vasey—Yaquina, Lincoln Co., July 17, 1915, *3122*.

*Agrostis longiligula* Hitchc.—Jetty, Lincoln Co., July 19, 1915, VanGundia, *3256*.

*Agrostis microphylla* Steud.—Wren, Benton Co., June 26, 1914, *1314;* Cottage Grove, Lane Co., July 14, 1914, *1353;* Corvallis, July 6, 1914, F. D. Bailey, *1436*.

*Avena sativa* L.—Newport, Lincoln Co., July 18, 1915, *3132;* Briton, Lincoln Co., July 19, 1915, G. VanGundia, *3088;* Marshfield, Coos Co., July, 1916, C. E. Owens; Myrtle Creek, Douglass Co., June 9, 1914, F. D. Bailey, *3162*.

*Calamagrostis canadensis* (Michx.) Beauv.—Clatskanie, Columbia Co., May 20, 1914, F. D. Bailey, *1580*.

*Calamagrostis hyperborea* Lange—Clatsop, Clatsop Co., Nov. 7, 1911, *1109*.

*Festuca elatior* L.—Elk City, Lincoln Co., Aug. 20, 1914, *1380*.

*Festuca subulata* Trin.—Ashland, Jackson Co., Sept. 10, 1914, *1561;* Mary's Peak, Benton Co., Aug. 15, 1914, *1572;* Elk City, Lincoln Co., Aug. 20, 1914, *1382*.

*Holcus lanatus* L.—Canby, Clackamas Co., July 21, 1911, *1182;* Philomath, Jan. 6, 1914, *3115*, *1133;* Cottage Grove, Lane Co., July 14, 1914, *3114;* Mouth of Salmonsberry River, Tillamook Co., July 17, 1915, G. VanGundia, *3085*, *3129;* Yaquina, Lincoln Co., July 17, 1915, *3112;* Jetty, Lincoln Co., July 19, 1915, G. VanGundia, *3130;* Eddyville, Lincoln Co., Aug. 10, 1915, Hoerner, *3090;* Grant's Pass, Josephine Co., Sept. 2, 1916, J. R. Weir, *227;* Portland, Jan. 9, 1914, *1139;* Elk City, Lincoln Co., Aug. 20, 1914, *1379*.

*Lolium multiflorum* Lam.—Near Gray Station, Linn Co., July 4, 1914, *1419;* Corvallis, July 6, 1914, *1435*, Sept. 20, 1914, *1554;* Newport, Lincoln Co., July 21, 1915, *3128*.

*Lolium perenne* L.—Corvallis, Aug. 3, 1914, *1412*, Sept. 1, 1914, *3127*.

*Panicularia elata* Nash—Clatskanie, Columbia Co., Aug. 11, 1913, F. D. Bailey, *1105*.

*Panicularia pauciflora* (Presl.) Kuntze—Orenco, Washington Co., June 13, 1914, *1388;* Neah-Kah-Nie Mt., Tillamook Co., Sept. 17, 1915, F. D. Bailey, *3258;* Portland, Aug. 21, 1915, E. Bartholomew, *5942* (Barth. Fungi Columb. *4973*).

This coronate-spored grass rust is evidently very common throughout western Oregon on native grasses. It is, however, not common in the Willamette valley on oats. All of the collections on that host are from near the sea coast.

DeBary (Monat. Akad. Wiss. 211. 1866) was the first to conduct cultures indicating the genetic connection with aecia on *Frangula* and *Rhamnus* in Europe. Since that time many European investigators have conducted culture experiments (Klebahn, Die Wirtsw. Rostp. 254–262. 1904).

In America this species has been cultured by Arthur (Bull. Lab. Nat. Hist. State Univ. Iowa 4: 398. 1898; Jour. Myc. 11: 58. 1905; Mycol. 4: 18. 1912) and Carleton (Div. Veg. Phys. & Path. U. S. Dept. Agr. 16: 48. 1899; Bur. Pl. Industry, U. S. Dept. Agr. Bull. 63: 15. 1904).

The only culture made with Pacific coast material was made in 1916 in this laboratory under the writer's direction, using telial material on *Agrostis exarata* sent to the writer from Corvallis by G. B. Posey. This was used to inoculate *Rhamnus Purshiana*, with

the development of pycnia and aecia. This host is the only one on which aecia have been collected in Oregon, and they are very abundant, as the number of collections indicates.

160. **Puccinia Romanzoffiae** sp. nov.

O. Pycnia not seen.

III. Telia chiefly hypophyllous and petiolicolous, crowded on confluent groups, 0.5–1 mm. across or covering extensive areas on the petioles, early naked, pulverulent, chestnut brown, ruptured epidermis noticeable; teliospores somewhat irregularly ellipsoid or oblong, 19–24 by 34–42 $\mu$, rounded above and below, not or scarcely constricted; wall chestnut brown, 2–3 $\mu$ thick, marked by large sparsely distributed irregular tubercles, thickened at apex by a low sub-hyaline umbo to 4–5 $\mu$, pore of lower cell at septum similarly thickened; pedicel colorless, short deciduous.

On Hydrophyllaceae:

*Romanzoffia sitchensis* Bong.—Mt. Jefferson, 8,000 ft., Aug. 14, 1914, H. P. Barss, *2539*, type.

This species is distinguished from other species on this family of hosts by the character of the markings of the teliospore. In *P. Hydrophylli* Pk. the teliospores are closely and finely verrucose while in *P. Phaceliae* Syd. & Holw. they are smooth. The character of the teliospores in the latter species suggests a correlation with *P. montanensis* (cf. 136) which has aecia on *Phacelia* and other members of the family Hydrophyllaceae.

161. Puccinia rubefaciens Johans. Bot. Centr. **28**: 394. 1886.

On Rubiaceae:

*Galium boreale* L.—Hilgard, Union Co., July 10, 1914, *1540;* Austin, Grant Co., Aug. 1916, J. R. Weir, *241*.

The teliospores of this micro-form are very similar in shape and size to those of the opsis-form *P. ambigua* (cf. 61) and the eu-form *P. punctata* (cf. 156). These three species on *Galium* doubtless represent a series of correlated forms.

162. Puccinia rugosa Billings, King's Rep. 40th Par. 914. 1871. (Not *P. rugosa* Speg. 1886.)

*Puccinia Troximontis* Pk. Bot. Gaz. **6**: 227. 1881.

*Puccinia Columbiensis* E. & E. Proc. Phil. Acad. **1893**: 153. 1893.

On Cichoriaceae:

*Agoseris laciniata* (Nutt.) Green—Corvallis, July 10, 1915, *3215*.

163. Puccinia Saxifragae Schlecht. Fl. Berol. **2**: 134. 1824.

*Puccinia curtipes* Howe, Bull. Torrey Club **5**: 3. 1874.

On Saxifragaceae:

*Saxifraga Marshallii* Greene—Hood River, May 16, 1915, *3268;* Mary's River, E. of Wren, Benton Co., April 17, 1915, *2617.*

*Saxifraga odontoloma* Piper—Corvallis, May 1, 1915, *3269.*

164. Puccinia Sherardiana Koern. Hedw. **16**: 19. 1877.

*Puccinia Malvastri* Peck, Bull. Torrey Club **12**: 35. 1885.

On Malvaceae:

*Sidalcea virgata* Howell—Corvallis, May 31, 1892, A. T. Mulford, *5*, Apr. 13, 1912, F. D. Bailey, *3354*, June 23, 1913, F. D. Bailey, *1128*, Apr. 8, 1914, *3352*, Apr. 29, 1914, G. B. Posey, *3353*, Apr. 30, 1915, *3071;* Newburg, Yamhill Co., Apr. 9, 1915, F. D. Bailey, *3072.*

165. Puccinia Sidalceae Holw. N. Am. Ured. 1: 67. 1907.

On Malvaceae:

*Sidalcea oregana* Gray—Klamath Co., July 10, 1903, E. B. Copeland, type.

This collection was distributed as *P. Sphaeralceae* E. & E. in Sydow's Uredineen *1782.*

166. Puccinia Stipae Arth. Bull. Iowa Agr. College Dept. Bot. **1884**: 160. 1884.

On Poaceae: II and III.

*Stipa comata* Trin. & Rupr.—Umatilla, Umatilla Co., July 11, 1914, *1369,* May 11, 1915, *3205;* Hermiston, Umatilla Co., May 12, 1915, *3206.*

This species has aecia on various genera of Carduaceae including *Aster, Solidago, Grindelia* and *Senecio,* as has been shown by Arthur (Jour. Myc. **11**: 63. 1905; Mycol. **4**: 19. 1912, **7**: 72. 1915). No aecial collections have been made in Oregon, though that stage is doubtless not uncommon in the eastern part of the state (cf. 69).

167. Puccinia subnitens Dietel, Erythea **3**: 81. 1895.

? *Aecidium Sarcobati* Pk. Bot. Gaz. **6**: 240. 1881.

On Chenopodiaceae: I.

*Sarcobatus vermiculatus* (Hook.) Torr.—Eastern Oregon, Aug. 1902, D. Griffiths (Vestergren, Micro. Rar. Sel. *852*).

On Poaceae: III.

*Distichlis spicata* (L.) Greene—LaGrand, Union Co., March, 1915, C. C. Cate, *3278;* Umatilla, Umatilla Co., July 11, 1914, *1367, 1373;* Moro, Sherman Co., Aug. 4, 1914, C. R. Ball, *1856.*

This remarkable species has aecia on a large number of hosts in the Polygonaceae, Chenopodiaceae, Amaranthaceae, Cruciferae, etc. as was first shown by Arthur (Bot. Gaz. **35**: 19. 1903; Jour. Myc. **11**: 54. 1905, **12**: 16. 1906, **13**: 197. 1907, **14**: 15. 1908; Mycol.

1: 234. 1909, 2: 225. 1910, 4: 18. 1912). Bethel (Phytopath. 7: 92–94. 1917) has also conducted very extensive cultures and proven the genetic connection with aecia on many hosts.

In 1915, Arthur (Mycol. 8: 135. 1916), using telial material sent by the writer collected by Mr. C. C. Cate at LaGrand, Ore., obtained the development of aecia on *Chenopodium album*. This is the only culture made with material from the Pacific coast.

The aecia on *Sarcobatus* are included here on the strength of culture work conducted by Arthur, in which he obtained aecia on that host using telial material on *Distichlis* from Nevada. The matter is complicated by the fact that Bethel (l. c.) finds that the aecia on this host in Colorado go to *P. luxuriosa* (cf. 124) and *P. subnitens* can not be made to infect *Sarcobatus*. It is possible that the two species represent closely related biological forms.

168. Puccinia Symphoricarpi Hark. Bull. Calif. Acad. Sci. 1: 35. 1884.

On Caprifoliaceae:

*Symphoricarpos albus* (L.) Blake—Corvallis, Oct. 17, 1909, F. L. Griffin, *1047*, July, 1910, *1086*, Aug. 1910, *1050*, May 4, 1912, *1087*, May 19, 1913, F. D. Bailey, *1158;* Sheridan, Yamhill Co., July 7, 1914, H. P. Barss, *1291*, July 8, 1916, H. P. Barss, *3396;* North slope Mt. Hood, Aug. 7, 1914, *1611;* Grant's Pass, Josephine Co., Sept. 3, 1916, J. R. Weir, *234;* Hood River, July 24, 1915, *3064*.

This micro-form is exceedingly abundant in western Oregon. This species is morphologically correlated with the telial stage of *P. abundans* (cf. 59), which has aecia on the same host, as has been pointed out by Travelbee (Proc. Ind. Acad. Sci. **1914**: 233. 1915).

169. Puccinia Taraxaci (Reb.) Plowr. British Ured. & Ustil. 186. 1889.

*Puccinia Phaseoli* var. *Taraxaci* Reb. Fl. Noem. 356. 1804.

On Cichoriaceae:

*Taraxacum Taraxacum* (L.) Karst.—Corvallis, June, 1910, *1117;* Bonneville, Multnomah Co., Aug. 10, 1910, *3078;* Ashland, Jackson Co., Sept. 10, 1914, *3074;* The Dalles, Wasco Co., July 1, 1914, *3073;* Talent, Jackson Co., June 22, 1915, G. B. Posey, *3077;* Newburg, Yamhill Co., Apr. 13, 1914, F. D. Bailey, *3076*.

170. Puccinia Toumeyi Syd. in Sacc. Syll. Fung. **16**: 299. Feb. 1902.

*Puccinia circinans* Ell. & Ev. Bull. Torrey Club **27**: 61. 1900. (Not *P. circinans* Fckl. 1869 or Dietel 1897.)

*Puccinia chasmatis* Ell. & Ev. Jour. Myc. 8: 15. May, 1902.

On Scrophulariaceae:

*Pentstemon* sp.—Canyon City, Grant Co., Aug. 26, 1914, W. E. Lawrence, *3185*.

171. Puccinia Trautvetteriae Syd. & Holw. in Sydow, Monogr. Ured. 1: 552. 1903.

On Ranunculaceae:

*Trautvetteria grandis* Nutt.—S. W. slope Mt. Hood, July 23, 1915, *3251*.

This interesting micro-form, known only from a few collections from the mountains of the northwestern states, has also been reported from Japan.

172. Puccinia triticina Erikss. Ann. Sci. Nat. VIII. 9: 270. 1899.

On Poaceae:

*Triticum aestivum* L.—Hood River, June 20, 1914, *1399*.

*Triticum ovatum* Rasp.—Myrtle Creek, Douglass Co., June 9, 1914, F. D. Bailey, *1407*.

*Triticum vulgare* L.—Lebanon, Linn Co., Aug. 2, 1913, F. D. Bailey, *1126;* Myrtle Creek, Douglass Co., June 9, 1914, F. D. Bailey, *1941;* Cottage Grove, Lane Co., July 14, 1914, *1676;* Corvallis, July 6, 1914, *3159*, *3160*, July 10, 1914, F. D. Bailey, *1677*, July 29, 1914, *1685;* Bend, Crook Co., Sept. 11, 1916, J. R. Weir, *201*.

This, the common leaf rust of wheat, is very abundant in western Oregon. The life history is unknown. In morphological characters, it resembles closely the forms on native grasses commonly referred to *P. rubigo-vera*, most of which are now included in *P. Clematidis* (cf. 85).

173. Puccinia universalis Arth. Jour. Myc. 11: 21. 1908.

*Aecidium Dracunculi* Thüm. Bull. Soc. Nat. Moscow. 58: 212. 1878. (Not *P. Dracunculi* Auers. 1850.)

On Carduaceae: I.

*Artemisia* sp.—White Pine,Baker Co., June, 1913, J. R. Weir, *120*.

On Cyperaceae: II, III.

*Carex multicaulis* Bailey—Grant's Pass, Josephine Co., May 5, 1887, Thomas Howell.

*Carex praegracilis* W. Boott. (*C. marcida* Boott.)—Redmond, Crook Co., July 2, 1914, *1425*.

*Carex Rossii* Boott.—Hood River, July 23, 1915, *3289*.

*Carex umbellata* Schk.—Hood River, July 23, 1915, *3282*.

This species has aecia on *Artemisia* as has been shown by Arthur (Jour. Myc. 14: 21. 1908; Mycol. 2: 224. 1910, 4: 16. 1912).

174. Puccinia urticata (Lk.) Kern, Mycol. 9: 214. 1917.

*Aecidium Urticae* Schum. Enum. Pl. Saell. 2: 222. 1803.

*Caeoma urticatum* Link, in Willd. Sp. Pl. 6$^2$: 62. 1825.

*Puccinia Urticae* Lagerh. Mitt. Bad. Ver. **2**: 72. 1889. (Not *P. Urticae* Barcl. 1887.)

*Puccinia Garrettii* Arth. Bull. Torrey Club **32**: 41. 1905.

On Urticaceae: I.

*Urtica Lyallii* S. Wats.—Philomath, April 26, 1914, *1829*, May 10, 1914, *2569;* Corvallis, May 1, 1915, *3052*.

On Cyperaceae: II, III.

*Carex Barbarae* Dewey (*C. laciniata* Boott.)—Grant's Pass, Josephine Co., Sept. 3, 1916, J. R. Weir, *250*.

*Carex magnifica* Dewey—Newberg, Yamhill Co., April 13, 1914, F. D. Bailey, *3009;* Clatskanie, Columbia Co., May 20, 1914, F. D Bailey, *3002;* Neah-Kah-Nie Mt., Tillamook Co., Sept. 17, 1915, F. D. Bailey, *3357*.

*Carex nebraskensis* Dewey—Andrews, Harney Co., Aug. 1901, Griffiths & Morris (Griffiths, W. Am. Fungi *339*).

*Carex rostrata* Stokes (*C. utriculata* Boott.)—Clatskanie, Columbia Co., May 20, 1914, F. D. Bailey, *3010;* Redmond, Crook Co., July 1, 1914, *1433*.

*Carex* sp.—Hood River, May 14, 1914, *3021*.

The connection of this *Carex* rust with aecia on *Urtica* was first shown by Magnus in 1872 (Vehr. Bot. var. Prov. Brandb. **14**: 11. 1872). Many other European investigators have confirmed Magnus results (Klebahn, Die Wirtsw. Rostp. 293. 1904).

In America Arthur has conducted numerous successful culture experiments with this species (Bot. Gaz. **29**: 270. 1900; **35**: 16. 1903; Jour. Myc. **8**: 52. 1902; **12**: 15. 1906; **14**: 14. 1908; Mycol. **2**: 223. 1910; **4**: 17. 1912). Kellerman has also conducted successful culture experiments (Jour. Myc. **9**: 9. 1903). None of the culture work, however, has been conducted with Pacific coast material.

175. Puccinia Veratri Duby, Bot. Gall. **2**: 890. 1830.

*Puccinia Veratri* Clinton, in Peck, Rep. N. Y. State Mus. **27**: 103. 1875.

On Onagraceae: I.

*Epilobium* sp.—Parkdale, Hood River Co., May 14, 1914, *1511*.

On Liliaceae: II, III.

*Veratrum californicum* Durand—The Meadows, Wallowa Co., Aug. 18, 1897, E. P. Sheldon, *8714*.

*Veratrum viride* Ait.—Calloway Station, Benton Co., June 28, 1901, E. R. Lake, *1131;* Parkdale, Hood River Co., May 14, 1914, *1279;* Hilgard, Union Co., July 10, 1914, *1934*.

The aecial collection is referred here with some confidence. It was made in the immediate vicinity of *Veratrum* plants showing fresh

uredinia. The aecia were somewhat old and no uredinia were found on other *Epilobium* plants in the vicinity. Tranzschel (Ann. Myc. 7: 182. 1909) established the connection of aecia on *Epilobium* with *P. Veratri*, obtaining his clew from the close morphological resemblance of the teliospores of this species to those of *P. Epilobii* DC. Bisby (Am. Jour. Bot. 3: 527–561. 1916) has pointed out the morphological similarity of this species with *Uromyces plumbarius* (cf. 201), *P. Epilobii*, *P. Epilobii-tetragoni* (cf. 99) and *P. Epilobii-Fleischeri*.

176. Puccinia Violae (Schum.) DC. Fl. Fr. **6**: 62. 1815.

*Aecidium Violae* Schum. Enum. Pl. Saell. **2**: 224. 1803.

On Violaceae:

*Viola adunca* J. F. Smith—Mary's Peak, Benton Co., May 21, 1915, *3223*.

*Viola glabella* Nutt.—Corvallis, Linn Co., April 16, 1912, *1081;* Corvallis, May 19, 1912, F. D. Bailey, *3198*, April 29, 1914, F. D. Bailey, *3164*, July 14, 1914, H. P. Barss, *2548;* Hood River, May 14, 1914, *3197;* Portland, Aug. 30, 1915, E. Bartholomew, *5978* (Barth. N. Am. Ured. *1677*); Sumpter, Baker Co., July 16, 1913, J. R. Weir, *186;* Mary's Peak, Benton Co., Aug. 15, 1914, *2547*.

*Viola nephrophylla* Greene—Hilgard, Union Co., July 10, 1914, *2557*.

*Viola rugulosa* Greene—Horse Creek Canyon, Wallowa Co., June 4, 1897, E. P. Sheldon, *8258*.

*Viola* sp.—N. slope Mt. Hood, Aug. 7, 1914, *2553*.

177. Puccinia Wulfeniae Diet. & Holw. Erythea **3**: 79. 1895.

*Puccinia Syntheridis* Ell. & Ev. Bull. Torrey Club **27**: 61. 1900.

On Scrophulariaceae:

*Synthyris rotundifolia* Gray—Philomath, April 20, 1912, *1146;* Corvallis, April 8, 1914, *1286*.

178. Tranzschelia punctata (Pers.) Arth. Résult Sci. Congr. Bot. Vienne 340. 1906.

*Aecidium punctatum* Pers. Ann. Bot. Usteri **20**: 135. 1796.

*Puccinia Pruni-spinosae* Pers. Syn. Fung. 226. 1801.

On Rosaceae:

*Amygdalus Persica* L.—Kiger's Island, Benton Co., Oct. 5, 1913, C. M. Scherer, *1825*.

*Prunus domestica* L. (Italian Prune)—Salem, Marion Co., Aug. 1909, *1062;* Yamhill Co., Sept. 9, 1911, *1040;* Corvallis, Oct. 29, 1914, G. B. Posey, *3110*.

This is not an uncommon disease of the prune, though apparently doing little damage. It is less common on the peach. No aecial collections have been made in the northwest.

Tranzschel (Trans. Bot. Acad. St. Petersb. **11**: 67–69. 1905) was the first to culture this species showing that aecia occur on *Anemone.*

In America Arthur (Jour. Myc. **12**: 19. 1906; **13**: 199. 1907) has shown that the aecia on *Hepatica* common in the eastern United States are genetically connected.

179. Uromyces aemulus Arth. Bull. Torrey Club **38**: 373. 1911.

*Nigredo aemula* Arth. N. Amer. Flora **7**: 241. 1912.

On Alliaceae:

*Allium validum* S. Wats.—Paisley, Lake Co., Aug. 1914, J. S. Elder, *1987.*

180. Uromyces amoenus Syd. Ann. Myc. **4**: 28. 1906.

On Carduaceae:

*Anaphalis margaritacea occidentalis* Greene—Hood River, July 23, 1915, *3243;* Crater Lake, Klamath Co., Sept. 9, 1916, J. R. Weir, *235.*

*Anaphalis margaritacea subalpina* Gray?—N. slope Mt. Hood, Aug. 7, 1914, *1613.*

181. Uromyces Armeriae (Schlechtd.) Lev. Ann. Sci. Nat. III, **8**: 375. 1847.

*Caeoma Armeriae* Schlechtd. Fl. Berol. **2**: 126. 1824.

On Plumbaginaceae:

*Statice armeria* L.—Newport, Lincoln Co., May 16, 1914, C. E. Owens, *1999,* July 18, 1915, *3018.*

This species differs from *U. Limonii* in the shorter, broader teliospores and the short mostly deciduous pedicel. The first collection mentioned bears aecia accompanied by uredinia, the second, uredinia and telia only. The rust is abundant on a cliff near the seashore. So far as we are aware this is the first record of this species in America.

182. **Uromyces Beckmanniae** sp. nov.

O and I. Pycnia and aecia unknown.

II. Uredinia amphigenous, scattered, elliptical, 0.5–0.8 mm. long, soon naked, pulverulent, cinnamon brown, ruptured epidermis noticeable; paraphyses none; urediniospores globoid or broadly ellipsoid, 19–24 by 23–30 μ, wall colorless or pale yellow, 2–2.5 μ thick, finely verrucose-echinulate, pores 8–10, scattered.

III. Telia amphigenous and culmicolous, scattered or crowded, oblong, 0.4–0.7 mm. across, often confluent to form crusts or lines, tardily naked, blackish brown; teliospores obovoid or ellipsoid, angular, 20–26 by 29–40 μ, apex rounded or angular, narrowed below; wall chestnut brown, 1–2 μ thick, smooth, but showing distinct longitudinal ridges, apex thickened, 3–6 μ, pedicel colorless or slightly tinted next to the spore, equalling the spore or usually deciduous.

On Poaceae:

*Beckmannia erucaeformis* (L.) Host.—Corvallis, Sept. 21, 1911, *1183;* south Mary's River, Sept. 30, 1914, *3144*, Oak Creek, July 29, 1915, *3145* type, Aug. 14, 1915, *3026*, May, 1916, G. B. Posey.

Evidently the most common rust in Oregon on this host. It differs from *U. Hordei*, which is in general a southern form not known on the Pacific coast, in the larger teliospores which show distinct longitudinal ridges. From *U. Jacksonii* (cf. 192) this species differs in the thickened apices of the teliospores. No clue is available as to the aecial host. The rust is difficult to separate from *Puccinia Rhamni* (cf. 159) in the uredinial stage.

183. Uromyces Brodieae Ell. & Hark., Harkness, Bull. Cal. Acad. Sci. 1: 28. 1884.

*Uromycopsis Brodieae* Arth. Result Sci. Congr. Bot. Vienne 345. 1906.

On Alliaceae:

*Brodiaea* sp.—Corvallis, May 4, 1912, F. D. Bailey, *3304*, April 25, 1915, *2625*.

This opsis-form is evidently common in western Oregon. The rust is usually found attacking the tips of the leaves early in the spring. Aecia usually predominate, the telia being inconspicuous and easily overlooked.

184. Uromyces carneus (Nees) Hariot, Jour. de Bot. 7: 376. 1893.

*Aecidium carneum* Nees; Funk. Krypt. Gew. Ficktelgeb. 25: 4. 1818.

*Uromyces lapponica* Lagerh. Bot. Nat. 1890: 274. 1890.

*Uromycopsis lapponica* Arth. Result Sci. Congr. Bot. Vienne 345. 1906.

On Leguminosae:

*Astragalus* sp.—Austin, Grant Co., Aug. 1915, J. R. Weir, *168*.

185. Uromyces caryophyllina (Schrank.) Wint. in Rab. Krypt. Fl. 1[1]: 149. 1881.

*Lycoperdon caryophyllinum* Schrank. Baier. Fl. 2: 668. 1789.

*Nigredo caryophyllina* Arth. N. Am. Flora 7: 246. 1912.

On Caryophyllaceae:

*Dianthus Caryophyllus* L.—Portland, Sept. 30, 1912, F. D. Bailey, *1089*, Dec. 19, 1912, F. D. Bailey, *1744;* Corvallis, Dec. 1910, *3181*.

186. Uromyces Fabae (Pers.) DeBary, Ann. Sci. Nat. IV, 20: 80. 1863.

*Uredo Fabae* Pers. Neues Mag. Bot. 1: 93. 1794.

*Nigredo Fabae* Arth. N. Am. Flora 7: 251. 1912.

On Leguminosae:

*Lathyrus obovatus* (Torr.) White?—Sumpter, Baker Co., July 16, 1916, J. R. Weir, *192;* Austin, Grant Co., Aug. 1915, J. R. Weir, *197.*

*Lathyrus oregonensis* White—Andrews, Harney Co., Aug. 1901, Griffiths & Morris (Griffiths, West. Am. Fungi *349a*); Spencer Creek, Klamath Co., July 10, 1903, E. B. Copeland (Syd. Ured. *1764*).

*Lathyrus pauciflorus* Fern.?—Klamath Falls, Klamath Co., Sept. 8, 1916, J. R. Weir, *203.*

*Lathyrus polyphyllous* Nutt.—Mt. Hood, Aug. 31, 1901, E. W. D. Holway.

*Lathyrus sulphureus* Brewer—Corvallis, May 9, 1914, *3226;* Ashland, Jackson Co., Sept. 10, 1914, *3320.*

*Lathyrus* sp.—Scotts, 7 mi. N. of Fort Klamath, Klamath Co., Sept. 20, 1913, E. P. Meinecke, *Cr D 10;* Glendale, Douglass Co., July 17, 1914, *1506;* N. Mt. Hood, Aug. 7, 1914, *1490,* Aug. 9, 1914, *1486;* Whitewater Forest Station, Aug. 12, 1914, H. P. Barss, *3248;* Garden Home, Multnomah Co., July 20, 1915, *3249.*

*Vicia americana* Muhl.—N. slope Mt. Hood, Aug. 7, 1914, *1489,* Aug. 9, 1914, *1485;* Corvallis, Sept. 21, 1914, *1545.*

*Vicia linearis* (Nutt.) Greene—Mary's Peak, Benton Co., June 20, 1910, *1501;* Philomath, June 20, 1910, *1502;* Newberg, Yamhill Co., April 13, 1914, *1525;* Springbrook, Yamhill Co., June 25, 1914, F. D. Bailey, *3238.*

*Vicia truncata* Nutt.—Bonneville, Multnomah Co., Aug. 10, 1910, *1179;* Hood River, May 14, 1914, *1527.*

*Vicia* sp.—Dothan, Douglass Co., Sept. 8, 1914, G. B. Posey, *1550.*

187. Uromyces fallens (Desmaz.) Kern, Phytopath. 1: 6. 1911.

*Uredo fallens* Desmaz. Pl. Crypt. 1325. 1843.

*Nigredo fallens* Arth. N. Am. Flora 7: 254. 1912.

On Leguminosae:

*Trifolium pratense* L.—Mary's Peak, Benton Co., June, 1910, *3094;* Springbrook, Yamhill Co., June 22, 1914, G. B. Posey, *3234;* Corvallis, July 15, 1914, G. B. Posey, *3093,* Oct. 26, 1914, G. B. Posey, *1983;* Parkdale, Hood River Co., Aug. 5, 1914, *3101;* Portland, Aug. 23, 1915, E. Bartholomew (Barth. Fungi Columb. *4788*).

188. Uromyces heterodermus Syd. Ann. Mycol. 4: 29. 1906.

On Liliaceae:

*Erythronium parviflorum* (Wats.) Goodding—Corvallis, April 13, 1912, F. D. Bailey, *1114.*

A short-cycle form not uncommon in the Rocky Mt. and Pacific coast regions.

189. UROMYCES HOLWAYI Lagerh. Hedwigia **28**: 108. 1899.

*Uromyces Lilii* G. W. Clinton; Peck, Ann. Rep. N. Y. State Mus. **27**: 103. 1875. (Not *U. Lilii* Kunze. 1873.)

*Nigredo Lilii* Arth. Résult Sci. Congr. Bot. Vienne 344. 1906.

ON LILIACEAE:

*Lilium parviflorum* (Hook.) Holzinger—Wren, Benton Co., July, 1911, W. E. Lawrence, *1144;* Hood River, May 9, 1915, *3044;* May 16, 1915, *2661;* Bridal Veil, Multnomah Co., May 18, 1915, *2659;* Portland, June 21, 1915, *3060.*

190. UROMYCES HYPERICI-FRONDOSI (Schw.) Arth. Bull. Minn. Acad. Nat. Sci. **2**[2]: 15. 1883.

*Aecidium Hyperici-frondosi* Schw. Schr. Nat. Ges. Leipzig **1**: 68. 1822.

*Nigredo Hyperici-frondosi* Arth. Résult Sci. Bot. Vienne 344. 1906.

ON HYPERICACEAE:

*Hypericum Scouleri* Hook.—Corvallis, June 24, 1914, F. D. Bailey, *1628*, July 29, 1914, *1476;* Hood River, June 20, 1914, *3372.*

This species has not been previously reported west of the Mississippi valley.

191. UROMYCES INTRICATUS Cooke, Grevillea **7**: 3. 1878.

*Uromyces Eriogoni* Ell. & Hark.; Harkness, Bull. Cal. Acad. Sci. **1**: 29. 1884.

*Nigredo intricata* Arth. N. Am. Flora **7**: 244. 1912.

ON POLYGONACEAE:

*Eriogonum compositum* Dougl.—The Dalles, Wasco Co., July 3, 1914, *1300;* Hood River, July 22, 1915, *3140.*

*Eriogonum microthecum* Nutt.—Redmond, Crook Co., July 2, 1914, *2537.*

*Eriogonum stellatum* Benth.—Wren, Benton Co., June 26, 1914, *1326;* Hilgard, Union Co., July 10, 1914, *1439.*

*Eriogonum umbellatum* Torr.—Mt. Hood, 7,000 ft. elev., Sept. 1, 1901, E. W. D. Holway, 6,500 ft., Aug. 9, 1914, *1481, 1493.*

*Eriogonum vimineum* Dougl.—Elgin, Union Co., Aug. 15, 1899, C. L. Shear (Ell. & Ev. Fungi Columb. *1470*).

*Eriogonum virgatum* Benth.—Grant's Pass, Josephine Co., July 13, 1887, Thomas Howell, from Phanerogamic specimen in the herbarium Missouri Bot. Gard.

*Eriogonum* sp.—Waloupi Canyon, Wallow Co., Aug. 18, 1897, E. P. Sheldon, *8727;* Hermiston, Umatilla Co., May 12, 1915, *3039, 3250;* Hood River Co., July 22, 1915, *3140.*

192. Uromyces Jacksonii Arth. & Fromme, Torreya **15**: 260. 1915.
On Poaceae:

*Agrostis Hallii* Vasey—Corvallis, Sept. 4, 1914, *1576*.

*Agrostis maritima* Lam.—Hood River Co., Aug. 26, 1915, E. Bartholomew, *5971* (Barth. Fungi Columb. *4992*).

*Deschampsia caespitosa* (L.) Beauv.—Toledo, Lincoln Co., July 19, 1915, *3194*.

*Deschampsia elongata* (Hook.) Munro—Orenco, Washington Co., June 13, 1914, *1396;* Corvallis, July 6, 1914, *2658*, type, July 29, 1914, *1438;* Glendale, Douglass Co., Aug. 17, 1914, *1408*.

*Hordeum jubatum* L.—Umatilla, Umatilla Co., July 11, 1914, *1376*.

*Hordeum nodosum* L.—Portland, May 21, 1914, F. D. Bailey, *1583*.

In addition to the above collections this species is now recognized on *Agrostis pallens* from California and *Muhlenbergia Lemmoni* from Arizona and New Mexico. Collections have also been made on *Deschampsia elongata* in Washington and on *Hordeum nodosum* in Washington and California.

193. Uromyces Junci (Desmaz.) L. Tul. Ann. Sci. Nat. IV, **2**: 146. 1854.

*Puccinia Junci* Desmaz. Pl. Crypt. 81. 1825.

*Nigredo Junci* Arth. N. Am. Flora **7**: 238. 1912.

On Carduaceae: I.

*Arnica cordifolia* Hook.—Austin, Grant Co., Aug. 1915, J. R. Weir, *190*.

On Juncaceae: II, III.

*Juncus balticus* Willd.—Redmond, Crook Co., July 2, 1914, *1426;* Umatilla, Umatilla Co., July 11, 1914, *1372;* Toledo, Lincoln Co., July 19, 1915, *3391*.

This species develops its aecia on various Carduaceae. In Europe cultures have been conducted by various authors, according to Klebahn (Die Wirtsw. Rostp. 329. 1904), showing that the aecia occur on *Pulicaria dysenterica* (*Inula dysenterica*).

In America Arthur (Mycol. **4**: 22. 1912, **7**: 77. 1915) has shown by culture experiments that aecia occur on *Carduus* and *Ambrosia*. The aecia on *Arnica* are referred here on morphological grounds.

194. Uromyces Junci-effusi Sydow, Monog. Ured. **2**: 290. 1910.

*Puccinia Junci* Schw. Trans. Am. Phil. Soc. II. **4**: 295. 1832. (Not *P. Junci* Desmaz. 1825.)

*Uromyces effusus* Arth. Jour. Myc. **13**: 193. 1907. (Not *U. effusus* DeToni. 1888.)

*Nigredo Junci-effusi* Arth. N. Am. Flora **7**: 239. 1912.

On Juncaceae:

*Juncus Bolanderi* Engelm.—Ashland, Jackson Co., Sept. 10, 1914, *2523*.

*Juncus ensifolius* Wikstr.—Minum River, Wallowa Co., Aug. 11, 1897, E. P. Sheldon, Aug. 20, 1897, *8751a;* Corvallis, Aug. 10, 1911, *1188*, July 29, 1914, *2522;* Philomath, Oct. 28, 1911, *1184*, *1185*, *1186*, Jan. 6, 1914, *1106;* Clatsop, Clatsop Co., Nov. 7, 1913, *1199;* Hood River Co., Aug. 5, 1914, *2521;* Ashland, Jackson Co., Sept. 10, 1914, *2524;* Newport, Lincoln Co., July 17, 1915, *3394*.

*Juncus Mertensianus* Bong.—Big Creek, Waldport, Lincoln Co., Aug. 23, 1915, F. D. Bailey, *3381*.

*Juncus orthophyllus* Cov.—Silver Lake, Lake Co., (?) Aug. 20, 1891, J. B. Lieburg, from Phan. spec. in N. Y. Bot. Gard. *765*.

*Juncus oxymeris* Engelm.—St. Johns, Multnomah Co., July 28, 1902, E. P. Sheldon, from Phanerogamic specimen in National Museum *11019*.

This species has not been connected with any aecial form. From field observations made by the writer in Oregon it seems probable that the aecia are to be looked for on *Aster*.

195. Uromyces Lupini Berk. & Curt. Proc. Am. Acad. 4: 126. 1858.

*Nigredo Lupini* Arth. Résult Sci. Congr. Bot. Vienne 344. 1906.

On Leguminosae:

*Lupinus laxiflorus* Dougl.—Garden Home, Multnomah Co., Aug. 1909, *1828*, July 20, 1915, *3240*.

*Lupinus rivularis* Dougl.—Springbrook, Yamhill Co., May 14, 1914, F. D. Bailey, *1528*.

*Lupinus* sp.—Mt. Hood, Aug. 31, 1901, E. W. D. Holway, Aug. 9, 1914, *3227;* Bonneville, Multnomah Co., Aug. 11, 1910, *1074*, *1088;* Philomath, May 10, 1914, *3108;* Springbrook, Yamhill Co., June 22, 1914, F. D. Bailey, *3111;* Jetty, Lincoln Co., July 19, 1915, VanGundia, *3131;* Newport, Lincoln Co., July 20, 1915, *3264;* Hood River, July 23, 1915, *3020;* Eddyville, Lincoln Co., Aug. 9, 1915, Hoerner, *3180*.

196. Uromyces Medicaginis Pass. in Thüm. Herb. Myc. Oecon. 156. 1874.

*Nigredo Medicaginis* Arth. N. Am. Flora 7: 256. 1912.

On Leguminosae:

*Medicago lupulina* L.—Albany, Linn Co., Aug. 1907, David Griffiths; Medford, Jackson Co., June 26, 1915, G. B. Posey, *3057*.

The aecia of this species in Europe have been shown by Schroeter (Krypt. Fl. Schl. $3^1$: 306. 1887) and by Trebaux (Ann. Myc. 10: 74. 1912) to occur on various species of *Euphorbia*.

No aecia in America have been found which can be referred to this species. There is, however, no evidence at present available for believing the American species different from the European.

197. Uromyces minimus Davis, Bot. Gaz. **19**: 415. 1894.

*Nigredo minima* Arth. Résult Sci. Congr. Bot. Vienne 344. 1906.

On Poaceae:

*Muhlenbergia comata* (Thurnb.) Benth.—Wallowa Valley, Wallowa Co., July 28, 1900, Wm. C. Cusick.

*Muhlenbergia racemosa* (Michx.) B.S.P.—Wallowa Valley, Wallowa Co., July 28, 1900, Wm. C. Cusick.

198. Uromyces oblonga Vize, Grev. **5**: 110. 1877.

*Uromyces minor* Schröt. Krypt. F. Schles. $3^1$: 310. 1887.

*Uromycopsis minor* Arth. Résult Sci. Congr. Bot. Vienne 345. 1906.

On Leguminosae:

*Trifolium albopurpureum* T. & G.—Corvallis, E. R. Lake, *3229*.

*Trifolium dubium* Sibth.—Corvallis, Apr. 10, 1914, F. D. Bailey, *1522;* Orenco, Washington Co., June 13, 1914, *3228;* Yaquina, Lincoln Co., July 17, 20, 1915, *3100;* Gerlinger, June 22, 1914, G. B. Posey, *3231*.

*Trifolium eriocephalum* Nutt.—Corvallis, July, 1910, *1989*.

*Trifolium Hallii* Howell—Corvallis, June 6, 1899, E. R. Lake, *3232*, May 12, 1903, A. H. Post, *3230*.

*Trifolium microdon* H. & A.—Corvallis, May 11, 1907, E. R. Lake, *1498*.

*Trifolium oliganthum* Steud.—Corvallis, May 11, 1914, F. D. Bailey, *2513*.

*Trifolium procumbens* L.—Corvallis, June 22, 1901, L. C. M., *1833*, July, 1910, *1176*.

*Trifolium tridentatum* Lindl.—Philomath, June 24, 1914, *1345;* Corvallis, May 28, 1903, E. R. Lake, *3236*, May 11, 1914, F. D. Bailey, *3235*.

This opsis-form is very common on native *Trifolium* sp. The original collection by Harkness was reported as occurring on "Bur cloves" now considered an error for *Trifolium*.

199. Uromyces occidentalis Diet. Hedwigia Beibl. **42**: 98. 1903.

*Nigredo occidentalis* Arth. N. Am. Flora **7**: 252. 1912.

On Leguminosae:

*Lupinus* sp.—Grant's Pass, Josephine Co., Sept. 3, 1916, J. R. Weir, *248*.

200. Uromyces perigynius Halsted, Jour. Myc. **5**: 11. 1889.

*Nigredo perigynia* Arth. Résult Sci. Congr. Bot. Vienne 344. 1906.

On Cyperaceae:

*Carex arthrostachya* Olney—Corvallis, July, 1910, *1191*, *1192*.

This species is morphologically indistinguishable from *P. Asterum* (cf. 69) in all spore stages except in the possession of one-celled teliospores. Like that species the aecia occur on *Aster* and *Solidago*. The genetic connection was established by Arthur in repeated experiments (Jour. Myc. 10: 16. 1904; Mycol. 4: 21. 1912, 7: 75. 1915, 7: 83. 1915). Fraser (Mycol. 4: 181. 1912) has confirmed Arthur's results in part.

The above collection is the only one so far known from the Pacific coast.

201. Uromyces plumbarius Peck, Bot. Gaz. 4: 127. 1906.

*Nigredo plumbaria* Arth. Résult Sci. Congr. Bot. Vienne 344. 1906.

On Onagraceae:

*Pachylophus marginatus* (Nutt.) Rydb.—Snake River, E. Oregon, June 3, 1901, W. C. Cusick (Phan. spec. *2542*).

*Pachylophus montanus* (Nutt.) A. Nels.—Crooked River, Crook Co., July 3, 1901, W. C. Cusick (Phan. spec. *2633*).

This species is correlated in morphological characters with *P. Epilobii-tetragoni* (cf. 99).

202. Uromyces Polygoni (Pers.) Fuckel, Symb. Myc. 64. 1869.

*Puccinia Polygoni* Pers. Neues Mag. Bot. 1: 119. 1794.

*Nigredo Polygoni* Arth. Résult Sci. Congr. Bot. Vienne 344. 1906.

On Polygonaceae:

*Polygonum aviculare* L.—Corvallis, Sept. 4, 1914, *1929;* Clatskanie, Columbia Co., Oct. 6, 1914, F. D. Bailey, *1945;* Medford, Jackson Co., June 20, 1915, G. B. Posey, *3055*.

203. **Uromyces porosus** (Peck) comb. nov.

*Aecidium porosum* Peck, Bot. Gaz. 3: 37. 1878.

*Uromyces coloradensis* Ellis & Ev. Erythea 1: 204. 1893.

*Uromycopsis porosa* Arth. Résult Sci. Congr. Bot. Vienne 345. 1906.

On Leguminosae:

*Vicia americana* Muhl.—Orenco, Washington Co., April 23, 1915, I, *1161*, June 13, 1914, III, *3237*.

The two collections were made at the same spot on different dates. The first consists of aecia only and the second of telia only.

204. Uromyces proeminens (DC.) Pass.; Rabh. Fungi Eur. 1795. 1873.

*Uredo proeminens* DC. Fl. Fr. 2: 235. 1805.

*Nigredo proeminens* Arth. N. Am. Flora 7: 259. 1912.

On Euphorbiaceae:

*Euphorbia glyptosperma* Engelm.—Wasco Co., July 23, 1885, W. N. Suksdorf (from Phan. spec. in N. Y. Bot. Gard.).

*Euphorbia oregonensis* Millsp.—Horse Creek Canyon, Wallowa Co., May 20, 1897, E. P. Sheldon, *8115*.

205. Uromyces punctatus Schröt. Abh. Schles. Ges. 48: 10. 1870.

*Nigredo punctata* Arth. N. Am. Flora 7: 253. 1912.

On Leguminosae:

*Astragalus Purshii* Dougl.—Austin, Grant Co., Aug. 1915, J. R. Weir, *236*.

The aecia of this species have been shown by European authors to occur on *Euphorbia cyparissias*. No aecial collections have been made in America.

206. Uromyces Scirpi (Cast.) Burrill, Bot. Gaz. 9: 188. 1884.

*Uredo Scirpi* Cast. Cat. Pl. Mars. 214. 1845.

*Nigredo Scirpi* Arth. Résult Sci. Congr. Bot. Vienne 344. 1906.

On Cyperaceae:

*Scirpus paludosus* A. Nels.—Waldport, Lincoln Co., Aug. 23, 1915, F. D. Bailey, *3323*.

This species was first shown by Dietel (Hedwigia 29: 149. 1890) to have its aecia on *Sium latifolium* and *Hippurus vulgaris*. Other investigators have added other Umbelliferous hosts to the list.

In America Arthur (Jour. Myc. 13: 199. 1907; 14: 17. 1908; Mycol. 1: 237. 1909) has shown that *Cicuta maculata* is an aecial host. Fraser (Mycol. 4: 178. 1912) has confirmed Arthur's work. Aecia on other hosts are properly referred here on morphological grounds. The species can doubtless be separated into a number of biological forms when more extensive culture work has been conducted.

207. Uromyces Silphii (Burrill) Arth. Jour. Myc. 13: 202. 1907.

*Aecidium compositarum Silphii* Burrill; DeToni in Sacc. Syll. Fung. 7: 798. 1888.

*Uromyces Junci-tenuis* Sydow, Monog. Ured. 2: 289. 1910.

*Nigredo Silphii* Arth. N. Am. Flora 7: 239. 1912.

On Juncaceae:

*Juncus occidentalis* (Cov.) Wieg.—Corvallis, Aug. 10, 1911, *1187*, June 24, 1914, F. D. Bailey, *1387*, July 29, 1914, *1445;* Philomath, Jan. 6, 1914, *1108*, May 10, 1914, *3393;* Hood River, July 24, 1915, *3392*.

Arthur (Jour. Myc. 13: 202. 1907; 14: 17. 1908) has shown that this common species has its aecia on *Silphium*. Using telial material on *J. tenuis* from Indiana, West Virginia and Nebraska, five successful

infections of *Silphium perfoliatum* were obtained, all of which resulted in the development of pycnia and aecia. The aecia on *Silphium* have been collected, so far as known to the writer, only in the Mississippi Valley from Ohio to Wisconsin, Kansas and Missouri, on three species of *Silphium*. The range of the telial collections referred here, however, is much greater including nearly the entire United States and Canada except the south Pacific slope. It seems probable that some plants other than *Silphium*, at present unrecognized, also serve as aecial hosts for this species.

208. Uromyces Solidaginis (Sommf.) Niessl, Verh. Natur.-Ver. Brüm. 10: 163. 1872.

*Caeoma Solidaginis* Sommerf. Suppl. Fl. Lapp. 234. 1826.

*Telospora Solidaginis* Arth. Résult Sci. Congr. Bot. Vienne 346. 1906.

On Carduaceae:

*Solidago* sp.—Dufur, Wasco Co., June 30, 1914, *1336*.

This is the only micro-Uromyces occurring in both Europe and America. This species shows a morphological correlation with *P. Asteris* (cf. 70).

209. Uromyces Spragueae Hark. Bull. Calif. Acad. Sci. 1: 36. 1884.

*Uromycopsis Spragueae* Arth. Résult Sci. Congr. Bot. Vienne 345. 1906.

On Portulaceae:

*Calyptridium roseum* Wats.?—Crater Lake, Klamath Co., 7,000 ft., Sept. 22, 1913, E. P. Meinecke, *CrPkD (2) 11*.

*Spraguea multiceps* Howell—Strawberry Mt., Grant Co., Sept. 2, 1913, W. E. Lawrence, *1177*.

210. Uromyces substriatus Sydow, Ann. Myc. 4: 30. 1906.

*Nigredo substriata* Arth. N. Am. Flora 7: 253. 1912.

On Leguminosae:

*Lupinus* sp.—Austin, Grant Co., Aug. 1915, J. R. Weir, *150*.

211. Uromyces Trifolii (Hedw. f.) Lev. Ann. Sci. Nat. III, 8: 371. 1847.

*Puccinia Trifolii* Hedw. f.; DC. Fl. Fr. 2: 225. 1805.

*Nigredo Trifolii* Arth. Result Sci. Congr. Bot. Vienne 344. 1906.

On Leguminosae:

*Trifolium hybridum* L.—Corvallis, Aug. 1909, *3092;* Hood River Co., May 14, 1914, *3091*, Aug. 5, 1914, *3095;* Portland, June 11, 1914, *3233;* Springbrook, Yamhill Co., June 22, 1914, G. B. Posey, *3103;* Garden Home, Multnomah Co., July 15, 1914, F. D. Bailey, *1508;* Grant's Pass, Josephine Co., Sept. 3, 1916, J. R. Weir, *217*.

212. Uropyxis sanguinea (Peck) Arth. N. Am. Flora 7: 155. 1907.
*Uromyces sanguineus* Peck, Bot. Gaz. 4: 128. 1879.
*Puccinia mirabilissima* Peck, Bot. Gaz. 6: 226. 1881.
On Berberidaceae:
*Berberis aquifolium* Pursh—Sauvies Island, Multnomah Co., Apr., 1882, Joseph Howell; Siskiyou, Jackson Co., May 31, 1894, E. W. D. Holway (Barth. N. Am. Ured. *1400*); Corvallis, March 26, 1908, C. C. Cate, *3382*, April 13, 1908, F. L. Griffin, *3383*, March 14, 1913, *1137;* Philomath, Jan. 1, 1914, *1153;* Tualetin, Washington Co., March 25, 1915, F. D. Bailey, *2616;* Grant's Pass, Josephine Co., Sept. 3, 1916, J. R. Weir, *182a.*
*Berberis pumila* Greene, Pokegama, Klamath Co., July 9, 1903, E. B. Copeland (Sydow, Ured. *1777;* Baker, Pacific Coast Fungi *3708*).

Form Genera

213. Aecidium Allenii Clinton in Peck, Rep. N. Y. State Mus. 24: 93. 1872.
On Elaeagnaceae:
*Lepargyrea canadensis* (L.) Greene—Strawberry Mt., Grant Co., Sept. 2, 1913, W. E. Lawrence, *1113;* Sumpter, Baker Co., June, 1913, J. R. Weir, *6;* Gold Center, July, 1914, H. F. Wilson, *1842.*

214. Aecidium Collinsiae Ell. & Ev. Bull. Washb. Lab. 1: 4. 1884.
*Aecidium Tonellae* D. & H. Erythea 3: 77. 1895.
On Scrophulariaceae:
*Collinsia parviflora* Lindl.—Philomath, April 20, 1912, *1169.*
This species is evidently an heteroecious form known otherwise only from Washington on the above host and on *C. Rattoni* and *C. tenella.*
It is apparently distinct from *P. Collinsiae* P. Henn. (Hedwigia 37: 269. 1898) as stated by Hennings. The aecia of the latter, judging from the description, arise from a limited mycelium. There is no evidence of telia in any of the collections of *A. Collinsiae* examined. *P. Collinsiae* has evidently been collected but once and material is not available for examination.

215. Aecidium columbiense Ell. & Ev. Erythea 1: 206. 1893.
On Cichoriaceae:
*Hieracium albiflorum* Hook.—Hood River, road to Lost Lake, May 16, 1915, *3245.*
*Hieracium* sp.—Bridal Veil, Multnomah Co., May 18, 1915, *3291.*
The aecia arise from a distributed mycelium and are not followed by any other stage. *Puccinia Hieracii* may however occur on the

same plants and even on the same leaves. Sydow (Ann. Myc. 1: 326. 1903) described *P. sejuncta* on such a mixture.

216. Aecidium Delphinii Barth. Jour. Myc. 8: 173. 1902.

*Aecidium Batesianum* Barth. in E. & E. Fungi Col. 1901. 1904.

On Ranunculaceae:

*Delphinium depauperatum* Nutt.—Mary's Peak, Benton Co., May 21, 1915, *3216*.

*Delphinium* sp.—Corvallis, April 11, 1915, *2615;* Redmond, Crook Co., May 15, 1915, *3327*.

This species is possibly identical with aecia on other Ranunculaceous hosts referred to *P. Clematidis* (cf. 85). For purposes of this list it is retained as a separate form as no cultures have been conducted.

217. Aecidium Graebnerianum Henn. Hedwigia 37: 273. 1898.

*Aecidium Alaskanum* Trelease, Harr. Alaska Exp. 5: 37. 1904.

On Orchidaceae:

*Limnorchis dilatata* (Pursh) Rydb.—Horse Lake, Cascade Mts., Aug., 1909, J. C. Bridwell, *3322*.

This unconnected *Aecidium* is doubtless heteroecious since no other stages have been found following the aecia on any of the collections examined. The species is known otherwise only from Alaska and in the mountains of British Columbia, Montana and California.

218. Peridermium Coloradense (Diet.) Arth. & Kern, Bull. Torrey Club 33: 426. 1906.

On Pinaceae:

*Picea Engelmanii* Parry—Whitman National Forest, Wallowa Co., July, 1913, J. R. Weir, *277*.

This species forms large witches' brooms.

219. Peridermium ornamentale Arth. Bull. Torrey Club 28: 665. 1901.

On Pinaceae:

*Abies concolor* (Gord.) Parry—White Pine, Baker Co., June, 1913, J. R. Weir, *145*.

*Abies nobilis* Lindl.—Larch Mt., Multnomah Co., Aug., 1910, *3293*.

220. **Uredo Phoradendri** sp. nov.

O. Pycnia not seen.

II. Uredinia amphigenous, gregarious, not crowded, spots not conspicuous, punctate; rounded or slightly elongated, 0.4–0.8 mm. across, tardily naked, somewhat pulverulent, bright orange, dehiscent by an elongate or irregular fissure of the epidermis, ruptured epidermis conspicuous and persistent; peridium membranous, at first hemispherical, remaining closely adherent to the ruptured epidermis,

made up of colorless isodiametric cells, 14–19 $\mu$ across, sometimes somewhat rhomboidal, smooth, wall 1–1.5 $\mu$ thick; urediniospores ellipsoid or obovoid, 17–33 by 26–32 $\mu$, wall colorless, 1.5–2.5 $\mu$ thick, very closely and minutely echinulate, pores very indistinct, 10–12, scattered.

III. Telia unknown.

On Loranthaceae:

*Phoradendron villosum* Nutt.—Corvallis, Sept. 21, 1915, C. E. Owens, *3377* type.

## Index to Species

Figures following the names refer to the species numbers in the list.
Synonyms are in italics. New names and combinations are in bold-face type.


Aecidium *abundans* 59
*Alaskana* 217
Allenii 213
*Aquilegiae* 85
*asperifolii* 67
*Asterum* 69
Barbarae 135
*Batesianum* 216
*Bellidis* 139
*Berberidis* 151
*Blasdaleanum* 35
*carneum* 184
*Cinerariae* 101
*Clematidis* 85
columbiense 116, 215
*columnare* 5
Collinsiae 214
*compositarum Bidentis* 140
*compositarum Silphii* 207
*conorum Piceae* 22
Delphinii 216
*Dracunculi* 173
*elatinum* 20
*Fendleri* 103
*fuscum* 57
*Galii ambigum* 61
*Geranii-maculati* 153
*Giliae* 150
Graeberianum 217
*Grossulariae* 109
*Helianthi-mollis* 112
*Holboellii* 117
*Hydrophylli* 136
*Hyperici-frondosi* 190
*Ligulariae* 101
*Majanthae* 125
*Mertensiae* 136
*monoicum* 135
*Myrtilli* 27
*nitens* 45
*Oenotherae* 146
*Ornithogalum* 63
Palmeri 143
*Peckii* 146
*Phaceliae* 136
*Pirolae* 22
*porosum* 203
*pseudo-balsameum* 32
*punctatum* 178
*Pyrolae* 29
*Rhamni* 159
*Sarcobati* 167
*Solidaginis* 69
*Sorbi* 43
*Tonellae* 214
*Tussilaginis* 100
*Urticae* 174
*Violae* 176
Allodus *ambigua* 61
*asperior* 68
*Calochorti* 76
*claytoniata* 84
*commutata* 89
*Dichelostemmae* 96
*Douglasii* 97
*Giliae* 150
*Jonesii* 122
*melanconioides* 128
*oregonensis* 68
*Palmeri* 143
Aregma *speciosa* 33
Ascophora *disciflora* 47

Bullaria *Angelicae* 62

Caeoma *Armeriae* 181
*asteratum* 69
*claytoniata* 84
*erigeronatum* 69
*Galii* 25
*hieraciatum* 115
nitens 45
*occidentalis* 13
*Solidaginis* 208
*urticatum* 174
Calyptospora columnaris 5
*Geoppertiana* 5
Chrysomyxa Abietis 6
*Pirolae* 22
Weirii 6
Coleosporium **Adenocaulonis** 1
asterum 4
Madiae 2
occidentale 3
Solidaginis 4
Cronartium *coleosporiodes* 7
*Comandrae* 8
filamentosum 7
pyriforme 8

Dicaeoma *asarinum* 66
*mesomegalum* 130

Earlea speciosa 33

Gymnoconia interstitialis 45
Gymnosporangium *asiaticum* 40
Betheli 34
Blasdaleanum 35
*chinense* 40
*Haraeanum* 40
Harknessianum 36, 39
juniperinum 37
juvenescens 38
Kernianum 39
koreaense 40
*Libocedri* 35
Nelsoni 41
nootkatensis 42, 43
Sorbi 43
tubulatum 44

Hyalopsora Aspidiotus 9
laeviuscula 10, 23
Polypodii 11

Kunkelia nitens 45

Lycoperdon *caryophyllinum* 185
*epiphyllum* 100
*poculiforme* 151

Melampsora albertensis 13, 18
arctica 14
Bigelowii 15, 16
**confluens** 16
Lini 17
Medusae 18
occidentalis 18
**Piscariae** 19
*sparsa* 30
sp. 12
Melampsorella *Cerastii* 20
elatina 20
Melampsoropsis Piperiana 21
Pyrolae 22
Milesia **Polystichii** 23

Nigredo *aemula* 179
*caryophyllina* 185
*Fabae* 186
*fallens* 187
*Hyperici-frondosi* 190
*intricata* 191
*Junci* 193
*Junci-effusi* 194
*Lilii* 189
*Lupini* 195
*Medicaginis* 196
*minima* 197
*occidentalis* 199
*perigynia* 200
*plumbaria* 201
*Polygoni* 202
*proeminens* 204
*punctata* 205
*Scirpi* 206
*Silphii* 207
*substriata* 210
*Trifolii* 211
Nyssopsora echinata 46

Peridermium *acicolum* 4
balsameum 31, 32
*Betheli* 8
californicum 2
coloradense 218
*conorum Piceae* 22

Peridermium *filamentosum* 7
Harknessii 7
*montanum* 4
ornamentale 219
Peckii 27
*pseudo-balsameum* 32
*pyriforme* 8
*Stalactiforme* 7
Phragmidium *affine* 49
disciflorum 47
imitans 48
Ivesiae 49
Jonesii 50
montivagum 51
occidentale 52
Potentillae 53
Rosae-acicularis 54
Rosae-californicae 55
*speciosum* 33
Pileolaria *brevipes* 56
Toxicodendri 56
Polythelis fusca 57
Puccinia Absinthii 58, 90
**abundans** 59, 168
Acetosae 60
*acuminata* 154
*Agropyri* 85
*albiperidium* 109
*alternans* 85
ambigua 61, 161
Andropogonis 143
Angelicae 62, 98
anomala 63
Antirrhini 64
*Archangelicae* 62
arnicalis 65
*Asari* 66
asarina 66
asperifolii 67
asperior 68
*Angelicae* 98
Asteris 70, 208
atro-fusca 71
Asterum 69, 200
atropunctata 110
*Bakeriana* 98
Balsamorrhizae 72
*Barbareae* 117, 135
*Bellidis* 139
bicolor 73
Bistortae 74
Blasdalei 75
Puccinia *Boisduvaliae* 99
Calochorti 76
Campanulae 77
canaliculata 140
*Caricis-Asteris* 69
*Caricis-Erigerontis* 69
*Caricis-Solidaginis* 69
*chasmatis* 170
Chelonis 78
Chrysanthemi 79
Cichorii 80
Cicutae 81
*cinerea* 85
circaeae 82
*circinans* 170
Cirsii 83
*Cirsii-lanceolati* 87
*cladophila* 111
*Clarkiae* 99
claytoniata 84
Clematidis 85, 107, 136, 172, 216
Clintonii 86
Cnici 87
*Columbiensis* 162
Collinsiae 214
Comandrae 88
*compacta* 94
commutata 89
conferta 58, 90
*congregata* 114
Convolvuli 91
*coronata* 88, 159
*Crandallii* 59
Crepidis-acuminatae 92
*curtipes* 163
Cyani 93
DeBaryana 94
Dentariae 95
Dichelostemmae 96
*difformis* 61
*dispersa* 67
Douglasii 97
Dracunculi 173
Ellisi 62, 98
Epilobii 175
Epilobii-Fleischeri 175
Epilobii-tetragoni 99, 175, 201
Eriophori 101
epiphylla 100
**Eriophyllii** 102
*extensicola* 69
**Fendleri** 103

Puccinia *Garrettii* 174
*Gayophyti* 99
Gentianae 105
*gemella* 104
Giliae 106
*glabella* 99
glumarum 107
*graminis* 103, 151
granulispora 108
Grossulariae 109, 144
grumosa 110
Harknessi 111
*Helianthi* 112
**Helianthi-mollis** 112
Hemizoniae 113
Heucherae 114
**hieraciata** 115
Hieracii 116, 215
Holboellii 117, 135
holcina 118
*Hordei* 63
Hydrophylli 160
Hypochoeridis 119
*inclusa* 83
**insperata** 120
Iridis 121
*Koeleriae* 103
Jonesii 122
*Junci* Desmaz. 193
*Junci* Schw. 194
*Kreageri* 59
Ligustici 123
*ludibunda* 146
*luteobasis* 123
luxuriosa 124, 167
*Madiae* 138
*Magnusii* 109
Majanthae 125
Malvacearum 126
*Malvastri* 164
*Mariae-Wilsoni* 84
McClatchieana 127
melanconoides 128, 141
Menthae 129
mesneriana 88
mesomegala 130
micromeriae 131
microsora 132
Millefolii 133
*mirabilissima* 212
monardellae 134
monoica 135
Puccinia montanensis 136
mutabilis 137
*neglecta* 107
*obliterata* 85
obscura 139
obtecta 140
*Oenotherae* 99
orbicula 120
*oregonensis* 68
**Ortonii** 141
*Osmorrhizae* 148
Oxyriae 142
Palmeri 143
Parkerae 144
*patruelis* 115
Pattersoniana 145
Peckiana 45
Peckii 146
Pentastemonis 147
Phaceliae 160
*Phaseoli* var. *Taraxaci* 169
*Phlei-pratensis* 151
Pimpinellae 148
Piperi 149
plumbaria 106, 150
*Poarum* 100
poculiformis 151
*Polygoni* 202
Polygoni-alpini 152
Polygoni-amphibii 153
porphyrogenita 154
*Potentillae* 53
*Pringsheimiana* 109
procera 155
*Pruni-spinosae* 178
punctata 61, 156, 161
pustulata 88
pygmaea 157
recedens 158
*recondita* 90
Rhamni 88, 118, 159
Ribis 144
*Richardsonii* 97
**Romanzoffiae** 160
rubefaciens 161
rubigo-vera 172
rugosa 162
Saxifragae 163
*sejuncta* 116, 215
*sessilis* 125
Sherardiana 164
Sidalceae 165

Puccinia *similis* 58
*simplex* 63
Sphaeralceae 165
*spreta* 114
Stipae 166
*straminis simplex* 63
subnitens 124, 167
Symphoricarpi 168
*Syntheridis* 177
Taraxaci 169
*Tiarellae* 114
*tomipara* 85
*tosta luxurians* 124
Toumeyi 170
Trautvetteriae 171
Treleasiana 104
*trifoliata* 148
*Trifolii* 211
triticina 172
*Troximontis* 162
*uniporula* 109
universalis 173
*Urticae* 174
Urticatum 174
Veratri 175
Violae 176
Wulfeniae 177

Pucciniastrum Abieti-Chamaenerii 24
Galii 25
Goodyerae 26
Myrtilli 27
pustulatum 24, 28
Pyrolae 29
sparsum 30
*Vacciniorum* 27

Roestelia *Betheli* 34
*Harknessiana* 36
*koreaensis* 40
*tubulata* 44

Telospora *Solidaginis* 208
Tranzschelia punctata 178
Tremella *juniperina* 37
Trichobasis *Balsamorrhizae* 72
*glumarum* 107
Triphragmium *echinatum* 46

Uredinopsis *Atkinsonii* 31
Copelandi 31, 32
Pteridis 32

Uredo *Acetosae* 60
*Angelicae* 62
*Artemisii* 58
*Aspidiotus* 9
*Betae Convolvuli* 91
*Chamaecyparidis-nutkaensis* 42
*Chimaphilae* 29
*Cichorii* 80
*coleosporiodes* 7
*confluens* 16
*Cyani* 93
*Dentariae* 95
*Fabae* 186
*fallens* 187
*Gentianae* 105
*glumarum* 107
*Goodyerae* 26
*Heucherae* 114
*Hieracii* 116
*Iridis* 121
*laeviuscula* 10
*miniata Lini* 17
*nootkatensis* 42
**Phoradendri** 220
*Pimpinellae* 148
*Polygoni Bistortae* 74
*Polypodii* 11
*proeminens* 204
*pustulata* 28
*quinqueporula* 151
*Scirpi* 206
*Solidaginis* 4
*vagans* α *Epilobii-tetragoni* 99
Uromyces Acetosae 60
aemulus 179
amoenus 180
Armeriae 181
*atro-fuscus* 71
**Beckmanniae** 182
Brodieae 183
carneus 184
caryophyllinus 185
*coloradensis* 203
*effusus* 194
*Eriogoni* 191
Fabae 186
fallens 187
heterodermus 188
Holwayi 189
Hordei 182
Hyperici-frondosi 190
intricatus 191

Uromyces Jacksonii 182, 192
Junci 193
Junci-effusi 194
*Junci-tenuis* 207
*lapponica* 184
*Lilii* 189
Lupini 195
Medicaginis 196
minimus 197
*minor* 198
oblonga 198
occidentalis 199
perigynius 200
plumbarius 175, 201
Polygoni 202
porosus 203
Uromyces proeminens 204
punctatus 205
*sanguineus* 212
Scirpi 206
Silphii 207
Solidaginis 208
Spragueae 209
substriatus 210
*Toxicodendri* 56
Trifolii 211
Uromycopsis *Brodieae* 183
*lapponica* 184
*minor* 198
*porosa* 203
*Spragueae* 209
Uropyxis sanguinea 212

## Host Index

Abies amabilis 32
balsamea 5, 14, 24
concolor 5, 219
Fraseri 5
grandis 5, 20, 24, 25, 31, 32
lasiocarpa 5, 20, 24
magnifica 5
nobilis 31, 219
pectinata 5
Abutilon? sp. 126
Achillea millefolium 133
Adenocaulon bicolor 1
Agoseris glauca 115
laciniata 162
Agropyron dasystachyum 85, 151
lanceolatum 85
spicatum 85, 145
tenerum 136
Agrostis alba 159
alba maritima 159
exarata 151, 159
foliosa 159
Hallii 192
longiligula 159
maritima 192
microphylla 159
pallens 192
Alopecuris californicus 151
Althaea ficifolia 126
rosea 126
Alliaceae 75, 96, 108, 137, 179, 183
Allium acuminatum 75
attenuifolium 75
Allium Geyeri 137
nevii 108
validum 179
Amaranthaceae 167
Amelanchier alnifolia 36
florida 35
Amygdalus Persica 178
Anacardiaceae 56
Anaphalis margaritacea occidentalis 180
margaritacea subalpina? 180
Anemone Drummondii 94
oregana 57
quinquefolia 57
Angelica atropurpurea 62
genuflexa 62, 98
Lyallii 62
tomentosa 98
Antirrhinum majus 64
Aquilegia formosa 85
truncata 85
Arabis sp. 135
Arbutus Menziesii 30
Arctostaphylos alpina 30
manzanita 30
nevadensis 30
Aristolochiaceae 66
Arnica cordifolia 65, 193
Artemisia dracunculoides 58
frigida 58
ludoviciana 58, 90
rigida 58
tridentata 58
Asarum caudatum 66

Aspidium Thelepteris 31
Aster acuminatus 69
conspicuus 4, 70
Cuseckii 4
Douglasii 4
folicaeus frondeus 4
Hallii 4
laevis geyeri 4
Astragalus sp. 184
Purshii 205
Athyrium cyclosorum 31
Avena fatua glabrata 151
sativa 151, 159

Balsamorrhiza deltoidea 72
sagittata 72
Beckmannia erucaeformis 151, 182
Berberidaceae 103, 212
Berberis aquifolium 103, 212
nervosa 103
pumila 212
Bidens connata 140
frondosa 140
Boisduvalia densifolia 99
glabella 99
stricta 99
Boraginaceae 136
Brodiaea sp. 183
*congesta* 96
Bromus carinatus 85
carinatus californicus 85
grandis 85
hordeaceus 85
hordeaceus leptostachys 85
marginatus 85
secalinus 85
tectorum 85
villosus 85
vulgaris 85

Calamagrostis aleutica 157
canadensis 159
hyperborea 159
Calochortus macrocarpus 76
Caltha biflora 104
Calyptridium roseum 209
Campanulaceae 77
Campanula rotundifolia 77
Scouleri 77
Caprifoliaceae 59, 168
Carduaceae 1, 2, 3, 4, 58, 65, 69, 70, 72, 79, 83, 87, 90, 93, 101, 102, 112, 113, 119, 133, 138, 158, 173, 180, 193, 208
Carex athrostachya 69, 200
Barbarae 174
canescens 69
Deweyana 69
Douglasii 71
festiva 69, 109
Goodenowii 69, 109
Hookeriana 146
Kelloggii 109
*laciniata* 174
magnifica 109, 174
*marcida* 69, 115, 173
mertensii 109
mirata 132
monile 109
multicaulis 173
nebraskensis 109, 174
phyllomanica 109
praegracilis 69, 115, 173
pratensis 115
rostrata 174
Rossii 173
scoparia 69
spectabilis 109
stipata 69
straminis 69
subfusca 69
trisperma 69
umbellata 173
*utriculata* 174
*vulgaris* 69
Caryophyllaceae 20, 185
Castilleja miniata 7
Centaurea cyanus 93
Cerastium oreophilum 20
viscosum 20
vulgatum 20
Chamaecyparis nootkatensis 42
Chamaenerion angustifolium 24
Chleone nemorosa 78
Chenopodiaceae 167
Chenopodium album 167
*Chimaphila occidentalis* 29
umbellata 29
Chrysanthemum sinense 79
Cichoriaceae 73, 80, 92, 111, 116, 120, 162, 169, 215
Cichorium intybus 80
Cicuta maculata 206
occidentalis 81

Circaea pacifica 82
Cirsium americanum 83
edule 83
lanceolatum 87
undulatum 83
Clarkia pulchella 99
Claytonia lanceolata 84
Clematis Drummondii 85
Douglasii 85
hirsutissima 85
ligusticifolia 85
Clintonia uniflora 130
borealis 130
Collinsia parviflora 214
Rattoni 214
tenella 214
Comandra umbellata 8, 88
Convallariaceae 130
Convolvulaceae 91
Convolvulus atriplicifolius 91
Cornaceae 154
Cornus canadensis 154
Crataegus Douglasii 34, 35, 44
Crepis gracilis 92
Cruciferae 95, 167
Cydonia vulgaris 35, 40
japonica 35
Cyperaceae 69, 71, 101, 109, 115, 127, 132, 140, 146, 173, 174, 200, 206

Dactylis glomerata 151
Delphinium depauperatum 216
Dentaria tenella 95
Deschampsia caespitosa 192
elongata 151, 192
Dianthus caryophyllus 185
Distichlis spicata 167
Dodecatheon alpinum 141
Hendersonii 141
Jeffreyi 141
latifolium 128
tetrandrum? 141

Elaeagnaceae 213
Elymus arenicola 155
condensatus 85
glaucus 85, 107, 136, 151
triticoides 85
virginicus 136
Epilobium adenocaulon 28
brevistylum 28
minutum 99
Epilobium paniculatum 99
Ericaceae 21, 30
Erigeron speciosus 69
Eriogonum compositum 191
microthecum 191
stellatum 191
umbellatum 191
vimineum 191
virgatum 191
Eriophorum angustifolium 101
polystachyon 101
viridi-carinatum 101
Eriophyllum lanatum 102
leucophyllum 102
*Eremocarpus setigerus* 19
Erythronium parviflorum 188
Euphorbia cyparissias 205
glyptosperma 204
oregonensis 204
Euphorbiaceae 19, 204
Euthamia occidentalis 69

Festuca confinis 59
elatior 151, 159
idahoensis 59
megalura 151
myuras 151
pacifica 149, 151
rubra 59
subulata 59, 159
Filix fragilis 11

Galium aparine 61, 156
asperrinum 156
boreale 161
triflorum 25, 156
Gaylussacia baccata 27
resinosa 27
Gayophytum ramosissimum 99
Gentiana oregana 105
Gentianaceae 105
Gilia gracilis 150
Godetia amoena 99
Goodyera Menziesii 26
Grindelia sp. 166
Grossulariaceae 16, 109

Helianthus annuus 112
Hemizonia truncata 113
Heuchera micrantha 114
Hieracium albiflorum 116, 215
cinereum 73, 116

Hieracium gracile 116
Scouleri 73, 116
Hierochloe macrophylla 151
Hippurus vulgaris 206
Holcus lanatus 118, 159
Hordeum distichon 151
Gussoneanum 107
jubatum 192
montanense 63
murinum 63
nodosum 63, 192
vulgare 63, 107, 151
Hookera pulchella 96
Hydrophyllaceae 136, 160
Hydrophyllum albifrons 136
capitatum 136
tenuipes 136
Hyperiaceae 190
Hypericum Scouleri 190
Hypochaeris radicata 119

*Inula dysenterica* 193
Iridaceae 121
Iris tenax 121
Ivesia Baileyi 50

Juncaceae 139, 193, 194, 207
Juncoides parviflorum 139
Juncus balticus 193
Bolanderi 194
ensiformis 194
mertensianus 194
occidentalis 207
orthophyllus 194
oxymeris 194
tenuis 207
Juniperaceae 34, 35, 37, 38, 39, 40, 41, 42
Juniperus chinensis 40
communis 41
occidentalis 34, 39, 41
scopulorum 34, 38, 41, 44
sibirica 37

Koeleria cristata 103, 135

Labiatae 129, 131, 134
Lagophylla ramosissima 112
Larix decidua 15
europea 15
occidentalis 15
Lathyrus obovatus 186
oregonensis 186
Lathyrus pauciflorus 186
polyphyllus 186
sulphureus 186
Leguminosae 184, 186, 187, 195, 196, 198, 199, 203, 205, 210, 211
Lepargyrea canadensis 213
Leptaxis Menziesii 114
Leptotaenia dissecta 68
Libocedrus decurrens 35
Ligularia sibirica 101
Ligusticum apiifolium 123
Cusickii 46
purpureum 46
Liliaceae 76, 110, 175, 188, 189
Lilium parviflorum 189
Limnorchis dilatata 217
Linaceae 17
Linum Lewisii 17
usitatissimum 17
Lolium multiflorum 151, 159
perenne 159
subulatum 151
Loranthaceae 220
Lupinus 199, 210
laxiflorus 195
rivularis 195
Lycopsis arvensis 67
Lygodesmia juncea 111

Madia citriodora 2
elegans 138
exigua 2
glomerata 2, 138
racemosa 2
ramosa 2
sativa 2
Malaceae 34, 35, 36, 37, 38, 40, 43, 44
Malus floribundus 35
Malva rotundifolia 126
Malvaceae 126, 164, 165
Medicago lupulina 196
Mentha canadensis 129
canadensis lanata 129
piperata 129
spicata 129
Mertensia laevigata 136
Micromeria chamissonis 131
*Douglassii* 131
Mitella Breweri 114
ovalis 114
Monardella odoratissima 134
villosa 134

Muhlenbergia comata 197
Lemmoni 192
racemosa 197

Nabalus hastatus 120
Navarettia intertexta 106

Onagraceae 24, 28, 82, 99, 175, 201
Orchidaceae 26, 217
Ornithogalum umbellatum 63
Narbonense 63
Osmorrhiza brevipes 148
divaricata 148
Liebergii 148
occidentalis 148
Oxycoccus macrocarpus 27
Oxyria digyna 142

Pachylophus marginatus 201
montanus 201
Panicularia elata 159
pauciflora 159
Pedicularis bracteosa 86
racemosa 86
Pentstemon sp. 170
diffusus 147
Menziesii 143
Peucedanum sp. 81
triternata 122
Phalaris arundinacea 125
Phacelia heterophylla 136
leucophylla 136
Phegopteris Dryopteris 9
Phleum pratense 151
Phlox condensata 97
diffusa 97
speciosa 150
Phoradendron villosum 220
Picea canadensis 22
Engelmanii 6, 22, 218
excelsa 30
mariana 22
Pinaceae 4, 5, 6, 7, 8, 13, 15, 20, 22, 24, 31, 32, 218, 219
Pinus contorta 4, 7
ponderosa 8
pungens 8
rigida 4
Piscaria setigera 19
Plumbaginaceae 181
Poa ampla 85, 100
annua 100
Poa fertilis 100
*Kingii* 59
macrantha 100
nemoralis 100
pratensis 100
triflora 100
trivialis 100
Poaceae 59, 63, 67, 85, 103, 107, 118, 124, 125, 135, 136, 145, 149, 151, 155, 157, 159, 166, 167, 172, 182, 192, 197
Polemoniaceae 97, 106, 150
Polygonaceae 60, 74, 142, 152, 153, 167, 191, 202
Polygonum alpinum 153
amphibium 153
aviculare 202
*emersum* 153
imbricatum 74
Muhlenbergii 153
Newberryi 74
pennsylvanicum 153
Polypodiaceae 9, 10, 11, 23, 31, 32
Polypodium occidentale 10
Polystichum munitum 10, 23
Populus acuminata 18
alba 12
angustifolia 18
balsamifera 18
candicans 18
tremuloides 13
trichocarpa 18
Portulaceae 84, 209
Potentilla aracnoides 53
blaschkeana 49
glomerata 49
gracilis 49
Hippiana 53
Primulaceae 128, 141
Prunus domestica 178
Pseudotsuga mucronata 13
Pteridium aquilinum pubescens 32
Ptiloria paniculata 111
Puccinellia nuttalliana 85
Pulicaria dysenterica 193
Pyrus baccata 35
communis 35
diversifolia 35
ioensis 35
malus 35
*rivularis* 35
sinensis 35, 40

Pyrola americana 22
elliptica 22
secunda 22, 29
Pyrolaceae 22, 29

Ranunculaceae 57, 85, 94, 104, 171, 216
Rhamnaceae 159
Rhamnus purshiana 159
Rhododendron californicum 21
Rhus diversiloba 56
Ribes divaricatum 109
lacustre 16, 109, 144
sanguineum 109
saxosum 16
vallicola 16
Romanzoffia sitchensis 160
Rosa gymnocarpa 33, 51, 55
nutkana 54, 55
pisocarpa 51, 55
Rosaceae 33, 45, 47, 48, 49, 50, 51, 52, 53, 54, 55, 100, 178
Rubiaceae 25, 61, 156, 161
Rubus leucodermis 48
neglectus 48
nigrobaccus 45
parviflorus 52
strigosus 48
vitifolius 45
Rumex acetosella 60
hastatulus 60
paucifolius 152

Salicaceae 12, 14, 15, 16, 18
Salix amygdaloides 15
argophylla 16
Bebbiana 14, 15
corda mackenzieana 15
cordata 15
discolor 14
fendleriana 14
lutea 14
Piperi 15
pseudocordata 15
scouleriana 15, 16
sitchensis 14
Sanicula bipinnata 68
Santalaceae 8, 88
Sarcobatus vermiculatus 124, 167
Saxifraga Marshallii 163
odontoloma 163
Saxifragaceae 114, 144, 163
Scirpus americanus 140
Scirpus microcarpus 127
paludosus 206
*pungens* 140
Scrophulariaceae 7, 64, 78, 86, 143, 147, 170, 177, 214
Secale cereale 67
Senecio aureus 101
ductaris 101
harfordii 158
hydrophiloides 3
palustre 101
triangularis 3
Sidalcea oregana 165
virgata 164
Silphium perfoliatum 207
Sitanion californicum 85
glabrum 85
hystrix 107
jubatum 85, 107
velutinum 85
Sium latifolium 206
Solidago sp. 208
canadensis 4
caurina 4
elongata 4
missouriensis 4
rugosa 4
tolmieana 4
Sorbus americana 37
aucuparia 35
hybrida 35
occidentalis 37, 43
sambucifolia 35
Sphaerostigma Boothii 99
dentatum 99
Sporobolus airoides 124
Spraguea multiceps 209
Statice Armeria 181
Stellaria borealis 20
Stenanthium gramineum 110
occidentale 110
Stipa comata 166
Symphoricarpos albus 59, 168
racemosus 59
Synthyris rotundifolia 177

Taraxacum Taraxacum 169
Tellima grandiflora 114
Thalictrum occidentale 85
Tiarella unifoliata 114
Trautvetteria grandis 171
Trifolium albopurpureum 198

Trifolium dubium 198
eriocephalum 198
Hallii 198
hybridum 211
microdon 198
oliganthum 198
pratense 187
procumbens 198
tridentatum 198
Triticum aestivum 107, 172
compactum 107, 151
diococcum 107
ovatum 172
vulgare 107, 151, 172
Tsuga canadensis 27
heterophylla 27
Tussilago farfara 100

Umbelliferae 46, 62, 68, 81, 98, 122, 123, 148
Urtica Lyallii 174
Urticaceae 174

Vacciniaceae 5, 27
Vaccinium caespitosum 27
Vaccinium canadense 27
macrophyllum 5, 27
myrtilloides 5
ovalifolium 5, 27
ovatum 5
parviflorum 5
pennsylvanicum 5
scoparium 5
Vitis-idaea 5
Valeriana occidentalis 89
Valerianaceae 89
Veratrum californicum 175
viride 175
Vicia americana 186, 203
linearis 186
truncata 186
Viola adunca 176
glabella 176
nephrophylla 176
rugulosa 176
Violaceae 176

Xanthium sp. 140

Zygadenus elegans 110

# EVOLUTION BY HYBRIDIZATION

EDWARD C. JEFFREY

*Harvard University*

Not long ago we were told that the investigation of the problems of evolution had left behind the inexact if broad phase of study in the field and had now entered upon the more accurate and satisfactory stage of quantitative elaboration under laboratory conditions. Leaving aside the question whether whatever exactitude in connection with this tendency has not been more than offset by a corresponding narrowness of outlook, it is now quite apposite to inquire if the experimental methods of the physiologist are in reality in the position to supply final light upon the fundamental problems of evolution. The judging of living beings by what they do rather than by what they are, has made notable progress in recent years. We are often told for example that an organ is the tool of a function and consequently should be defined by its performance rather than by its organization. I need not point out the essential fallacy of the physiological definition of an organ cited above. It obviously breaks down the moment it is used on any wide range of facts.

Perhaps the most striking illustration of depending overmuch upon physiological data is supplied in connection with present investigations upon the all important question of the origin of species. It is practically universally assumed in genetical studies, that the capacity to breed true under exacting experimental conditions is the most reliable criterion of good species. It has for example assumed that breeding results obtained with *Oenothera* and *Drosophila* are of fundamental importance for the science of biology. By those of us who have neither been intoxicated with the cult of the evening primrose nor bowed the knee in the temple of the god of flies, this conclusion will in general be held undemonstrated. We must obviously know a good deal more about the antecedents of those forms which have been raised in recent years to the dignity of veritable biological touchstones, before we can admit the validity of the far-reaching conclusions drawn from their genetical behavior.

The question of the origin of the species is as much with us today as it was at the time of the publication of Darwin's epoch-making work. Darwin himself ultimately ventured no explanation of the causes of the changes concerned in the formation of new species, but

contented himself mainly with pointing out that a general process of variation has been going on from age to age in matter endowed with life. He emphasized the fact that the struggle for existence on the one hand and the selection exercised by environment on the other provided an important directing influence upon the development of new species of plants and animals. In recent years a doctrine of old standing has been revived, namely the hypothesis of mutation. It has been maintained that new forms or elementary species arise spontaneously from formerly existing species. This doctrine has been particularly advanced by the activities of the Dutch physiologist De Vries and his disciples in this and other countries. It is a general observation in connection with the activities of the lower organisms that in the process of their often extremely active development they give rise to inhibiting substances. In the case of the common yeast for example we have the formation of alcohol, which finally, by a high degree of concentration in fermenting sugary solutions, brings the activity of the yeast organism to a close. It is of interest to note in this connection that it is precisely in Holland that scientific opposition to the mutation hypothesis of De Vries has recently appeared. To Dr. Lotsy we owe a recent volume on Evolution by Means of Hybridization, which attacks the mutation hypothesis at its very base through the contrary hypothesis that all changes in living matter are due to crossing or hybridization and are not the consequence of spontaneous internal or mutational phenomena. The author argues that since hybrids are notoriously variable all variability must be due to hybridism. This appears to be reasoning in a vicious circle. Clearly the most definite evidence in regard to hybridism as the cause of new species should be demanded before the possibility of the appearance of new types in this manner can be admitted. We fortunately have extremely good testimony on this subject from the earlier investigations published by Kerner in Austria and Brainerd in this country. Kerner in his well-known Pflanzenleben as well as in an earlier publication in the Oesterreiche Botanische Zeitung has brought forward much evidence as to the origin of new species as the result of hybridization in the mountainous regions of eastern central Europe, where the floras of the Pontic, Mediterranean and Baltic areas meet. It is impossible within the time at my disposal to make more than a very brief reference to the results reached by this writer. He has made it clear that the members of different floras are very apt indeed to produce new species by hybridization in nature and that these species, where they are advantageously equipped as compared with the parent forms, flourish within the same region. In case they have qualities which enable them to live where the parental species

are not able to survive successfully they are found to the exclusion of one or both of these. This last conclusion upsets the conventional assumption that hybrids can only exist where their originating species occur side by side. It is clear from the general results of the highly important systematic and geographical investigations of Kerner that new species may appear as the result of spontaneous hybridization.

The more recent evidence supplied by the investigations of Brainerd upon the violets and certain Rosaceae point equally positively in the same direction. This author has made it clear that a number of recognized species of *Viola* and *Rubus* are in reality hybrids in their origin. A particularly interesting result reached by Dr. Brainerd is that these hybrid species may become absolutely fixed in spite of their mode of origin and respond not only to recognized systematic but also to genetical criteria for species.

It is too often assumed at the present time that the best criteria of species are physiological. On this basis the capacity to breed true in cultures and to produce offspring which comply with the tests of genetical analysis is regarded as of paramount importance. Since many known hybrids comply equally with recognized species with these tests it has become clear that what a plant does in cultures cannot be accepted as an infallible evidence of its antecedents. Where physiological criteria fail, we turn to the more constant ones furnished by morphological characters. It has been recognized for nearly a century that sterility is often a marked feature of hybrids, especially when they result from the crossing of somewhat incompatible species. The causes of incompatibility are apparently unknown as often species more different in their external characteristics and more widely separated in geographical range can be crossed with greater success than those nearly related on the evidence of external features and geographic coincidence. For example the horse and the zebra produce fertile hybrids, while the horse and the ass, when crossed, give rise ordinarily to infertile mules. Similarly our common canoe, yellow and black birches, which often grow side by side without hybridizing all apparently cross with a considerable degree of readiness with the more isolated shrubby birch of swamps, *Betula pumila*, according to the investigations of Jack and Rosendahl in this country.

Hybrids may present in the case of plants a number of interesting morphological characteristics. For example we frequently find a high degree of imperfection in their gametic cells, male and female, with the emphasis of sterility nearly always on the male. This feature is often so marked that it is impossible to fertilize a hybrid with its own pollen, even when the ovules present a considerable degree of fertility. The morphological imperfection in pollen grains can obvi-

ously be most easily estimated and varies in proportion from a small percent to complete sterility. The sterility resulting from hybridization should not be confused, as sometimes happens, with sterility arising from purely physiological causes. For example the common horse radish, *Lilium bulbiferum* and *L. candidum*, under ordinary conditions do not set seed, by reason of the fact that the assimilates are too strongly determined to the subterranean parts to permit of the necessary materials being set free for the formation of seeds. It has been found however that the girdling the top of the subterranean stem in the horse radish or cutting off the flowering axis in the case of the lilies, brings about the formation of normal seeds. Similarly very marked climatic change or subjection to starvation or other extremely unfavorable physiological conditions results in the degeneracy of reproductive as well as other parts. Conditions like these are, however, very easily distinguished from the sterility normally resulting from hybridization.

Sterility in hybrids is of particular interest from the genetical standpoint because it more or less completely upsets the expectancy of Mendelian ratios in cultures of the offspring of species hybrids. This is doubtless one of the causes why the Mendelians have in general manifested so little interest in the genetical study of hybrids between natural species. Obviously however if the crossing of species in nature is a common cause of the origin of new species this part of the evolutionary field cannot be safely neglected if we are to reach any broad and permanently valid conclusions as the *modus operandi* of the origin of species.

Another feature in the organization of hybrids is the frequent increase in the typical generic chromosome number as a consequence of crossing. For example we find in the much crossed oriental species of *Chrysanthemum* a number of chromosomes in the gametic nuclear divisions varying from 9 (the normal) to 18, 27, 36, and even 45, in other words, two, three, four and five times the normal gametic number. Similarly in another compositaceous genus *Dahlia* we find in the species *D. coronata* sixteen chromosomata in gametophytic divisions while in the hybrids between *D. variabilis* and *D. coccinea* thirty-two chromosomes have been enumerated. One further example will point the situation. In the monotypic *Liriodendron* and in certain species of *Magnolia*, nineteen gametophytic chromosomes have been counted, while in *M. soulangeana* (suspected of hybrid origin) as well as *M. Yulan* and *M. grandiflora* twice that number or more of chromosomes have been observed. If we contrast the situation in these examples with that presented by the genera *Pinus* and *Lilium*, which are not at all prone to hybridism, we note a curious contrast. In the

species of the pine or lily, the chromosomes are always of the same number and do not vary as in the examples cited above, as occurring in connection with hybridism. Frequently the addition of chromosomes under hybrid conditions is not simply a doubling, tripling, etc., of the original number but a mere arithmetical addition. Among the vascular cryptogams and the mosses similar cases of multiplication of the normal number of chromosomes are frequently found in species growing in very damp situations or actually in the water and in which hybridization is accordingly favored.

Having enumerated a few of the morphological characteristics of hybrids we are now in the position to apply the facts elucidated to the case of the Oenotheras, which have been brought particularly into prominence in connection with the mutation hypothesis of De Vries. In the so-called mutants of *Oenothera lamarckiana* as well as in that species itself, we find all the cited stigmata of hybridism as presented by incompatible species, namely a high degree of sterility, amounting in some cases to complete impotency, particularly in the male gametic cells, failure to segregate in accordance with Mendelian ratios and the multiplication of the number of chromosomes beyond the normal gametophytic number seven, or sporophytic fourteen. In *O. gigas* the gametophytic chromosomes are 14 instead of the normal seven, while in *O. semigigas* there are 21 in the sporophyte instead of the normal fourteen and in *O. lata*, *O. semilata* and *O. rubricalyx*, fifteen. Similar conditions have been described in many other species of *Oenothera* and their so-called mutants. It accordingly appears abundantly clear when morphological considerations are brought into court as well as the physiological data derived from experimental breeding that the genus *Oenothera* is obviously affected by contamination through hybridization in its various species and their so-called mutants. The conclusion may accordingly be drawn that so far as the genus *Oenothera* throws light upon the origin of new species at all, it vouches rather for the multiplication of species as a consequence of hybridization than for their appearance as a result of the mysterious process of mutation.

In conclusion we may turn to an objection which has been raised by De Vries and other mutationists to the interpretation of morphological sterility as an evidence of hybridization. It has been claimed that this feature is an accompaniment of mutation. It is most unfortunate for the mutationists that a phenomenon so generally recognized as associated with the crossing of species should at the same time occur in mutating forms. The burden of proof that such forms are not of hybrid origin distinctly lies with the mutationists. We have however positive evidence that this is not a possible interpre-

tation. In monotypic genera such as *Ginkgo*, *Liriodendron*, *Calla*, *Spathyema*, etc., the pollen grains under normal physiological conditions of development are all alike and perfect. In Fig. 1, Plate V, is shown the pollen of *Zannichellia palustris*, a species isolated in our northern North American flora. It is clear that the grains are strikingly uniform and are all well developed. For comparison with the genus just mentioned which has very few species and consequently cannot be considered as highly variable, let us take the common pondweed *Potamogeton*, of which there are very many species. Fig. 2 shows the situation in the large genus just mentioned. The cells are not by any means all perfectly developed and are conspicuously characterized by extreme variations in size. It might be maintained on this basis of the illustrations furnished in Figs. 1 and 2 alone that variability in size of pollen grains is associated with the multiplication of species or in other words with the phenomenon of mutation. Against this view in the forms under discussion may properly be urged the fact that many natural hybrids between species of *Potamogeton* are known which manifest the usual morphological features of such forms.

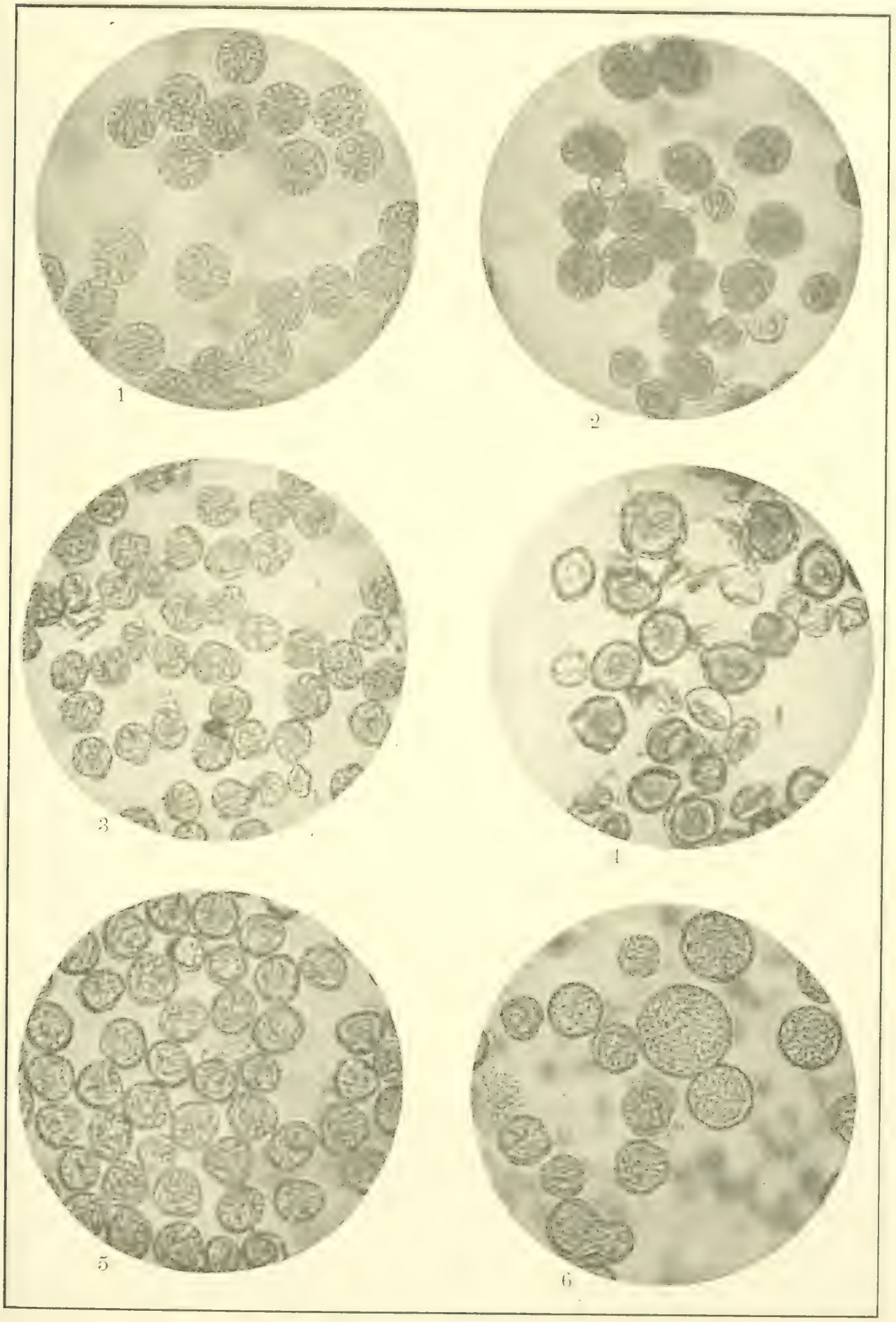
A clearer elucidation of the situation is furnished by the conditions in large genera, where a number of the species coincide both in geographical distribution and in the time of flowering. As a first illustration in this connection may be taken the genus *Rubus*, which has recently been investigated by Dr. Hoar. Fig. 4 shows the condition of the contents of the anther in *R. villosus*. Clearly the pollen varies greatly in size and perfection of development. A similar condition has been described by the author just cited in a large number of the species of *Rubus*. The general situation might be interpreted in view of the very numerous and at the same time very variable species of *Rubus* as an argument for the correlation of mutation and pollen sterility. When however the facts in species of the genus, which are in some manner isolated, are examined quite a different light is thrown on the subject. Fig. 3, Plate V, illustrates the pollen of *R. odoratus*, the flowering raspberry, which opens its blossoms at a considerably later period than the mass of the species of the genus. Care has been taken to include as large a number as possible of the grains in the field of view. It is obvious that the variation in size and frequent defective development of unisolated species of *Rubus*, are conspicuous by their absence. If irregularities in the development of the contents of the anthers were a feature correlated with mutation in the genus *Rubus* then we ought to find it equally present in isolated and unisolated species. Since that is not the case, the natural inference is that the sterility present in the pollen of species subject to hybrid contamina-

tion by reason of their coincidence of flowering periods, is actually the result of previous specific crossing. This view of the matter is strongly confirmed by the fact that the investigations of Brainerd and others on that genus have revealed a large number of natural hybrids.

For a parallel case we may now turn to the genus *Ranunculus*. If any of the species which flower in the early summer are examined, such as *R. acris*, *R. repens*, *R. aquatilis*, *R. Cymbalaria*, a considerable proportion of imperfect pollen is usually present and frequently the grains vary extremely in size. This situation is shown for *R. acris* in Fig. 6, Plate V. Obviously there is a great range of size in the grains and some are imperfect. This condition is most naturally interpreted as a consequence of previous hybridization. Fig. 5, Plate V, illustrates the condition of the pollen in *R. rhomboideus*, a species which flowers in the very early spring long before the other species of the genus have opened their blossoms. The numerous grains shown in the illustration are clearly well developed and somewhat uniform in size. In the species under consideration as well as in *R. odoratus*, perfection in development of pollen is clearly correlated with isolation from possibility of contamination with other species.

In view of the facts supplied in the above instances, which might be almost indefinitely multiplied in representatives of other angiospermous families, it appears clear that the obvious interpretation of pollen sterility is to be adopted, namely as an indication (where it occurs under normal conditions of growth) not of mutability but of previous hybridization. The large situation which is so briefly illustrated by the accompanying photographs, indicates the necessity of bringing morphological criteria relating to the cytology and development of the gametic cells (pollen and embryo sacs) into court, as well as the data derived from genetical behavior, in speculations in regard to the origin of species.

It seems clear from the evidence supplied on the systematic and phytogeographical sides on the one hand and that from the standpoint of morphology on the other, that the crossing of species in nature is an extremely common cause of the multiplication of species. It is further obvious that physiological and genetical criteria must not be given greater weight than the more reliable ones supplied by actual history and by morphological structure, in the all-important biological question of the origin of the species. It is finally apparent that the genetical status of the Oenotheras is so dubious that they cannot be brought into court to furnish decisive evidence in favor of the mutation hypothesis of De Vries. It may be added in conclusion that the multiplication of species by hybridization does not by any means invalidate the Darwinian hypothesis but merely supplies an additional




JEFFREY: EVOLUTION BY HYBRIDIZATION

agency for the formation of species. It appears moreover logically impossible to regard hybridization as the universal and sole cause of the appearance of new species, as has been recently maintained by Lotsy in his Evolution by Means of Hybridization, since the original species must have come into existence by some other means than by hybridization. The adaptation of the floral structures of the Angiosperms to cross fertilization, emphasized many years ago by the Austrian botanist Kerner is doubtless of significance in connection with the ever-increasing volume of evidence for the wide occurrence of natural hybrids in this large and successful group of seed-plants which have to so notable a degree furnished the facts for the existing general biological theories.

## DESCRIPTION OF PLATE V

FIG. 1. Pollen of *Zannichellia palustris*, showing great uniformity in a species unable to hybridize. × 400.

FIG. 2. Pollen of *Potamogeton diversifolius*, showing great diversity of size and development in pollen of a species subject to hyridization. × 400.

FIG. 3. Pollen of *Rubus odoratus*, a species which flowers late and consequently is not subject to crossing. × 400.

FIG. 4. Pollen of *Rubus villosus*, a species flowering with a number of others and consequently subject to hybridization. × 400.

FIG. 5. Pollen of *Ranunculus rhomboideus*, showing uniformity in a species exempt from crossing by early date of flowering. × 400.

FIG. 6. Pollen of *Ranunculus acris*, a species flowering at the same time as a number of others and consequently exposed to hybridization. × 400.

# A METHOD OF OBTAINING ABUNDANT SPORULATION IN CULTURES OF MACROSPORIUM SOLANI E. & M.

L. O. KUNKEL

*Bureau of Plant Industry, U. S. Department of Agriculture*

Although the early blight fungus, *Macrosporium solani*, often fruits abundantly when growing as a parasite on potato leaves, it usually does not bear very many spores when grown in pure culture. Jones (4) reports that some of his cultures when old fruited rather freely. Jones and Grout (5) state, however, in their technical description of the organism as *Alternaria solani* (E. & M.) Sorauer that it sporulates "sparsely in pure cultures."

Enough spores may be obtained by growing it in the ordinary way on culture media to test its parasitism to the potato plant. Galloway (3) performed this experiment as early as 1893 and Jones (4) repeated it a few years later. Nevertheless, the failure to obtain spores in quantity from pure cultures has made it impossible to perform extended infection experiments with this important parasite.

The writer found *M. solani* doing considerable damage in the potato fields of Aroostook County, Maine, last August, and in the hope of obtaining a strain of this fungus that would fruit abundantly in pure cultures, a considerable number of isolations were made. Cultures were in each case made from single spores. The organism was isolated from fifty-four different potato plants selected at random in half a dozen potato fields in the vicinity of Presque Isle, Maine. All of these single-spore strains were grown on a number of different culture media, including potato agar, string-bean agar, prune agar, and glucose agar. The several strains showed considerable differences in the appearance of their growth in culture, but none of them produced more than an occasional spore on any of the media tested.

In a former paper the writer (6) has described a method of retarding the growth of *Monilia sitophila* (Mont.) Sacc. by lowering the vapor tension of the atmosphere above pure cultures. It was recalled that by checking the mycelial growth in this way the fungus could be made to fruit more abundantly than when grown in a moist atmosphere. In the hope that this method might serve to induce sporulation, cultures of *M. solani* were subjected to like treatment. More spores

were obtained in these cultures than when the atmosphere above the fungus growth was allowed to remain near saturation. It was found, however, that this method of treatment would not bring about very abundant sporulation in the case of the early blight organism. A number of other methods were tested, and the idea of wounding the mycelium was finally hit upon. This seems to be the stimulus necessary to bring about abundant sporulation in cultures of *M. solani*. It will fruit profusely on any of the media above mentioned if the mycelium is thoroughly wounded after the culture is two or three days old and has made a good start. So long as the mycelium is undisturbed it grows very vigorously through and over the surface of most culture media. In these cultures very few conidiophores are produced and very few spores are developed. Undisturbed cultures often fail to

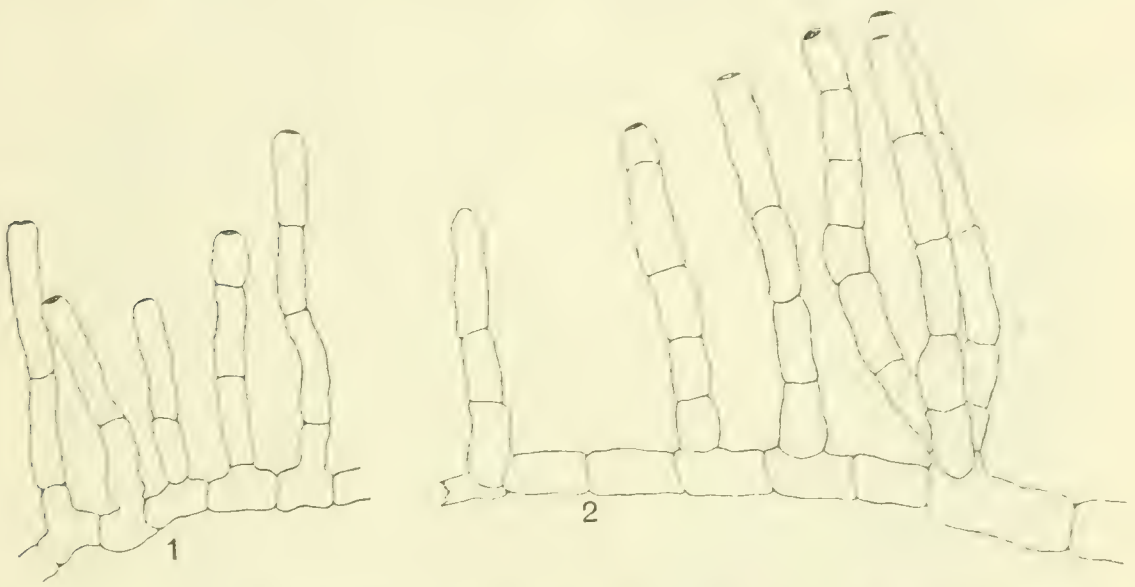



FIG. 1. A wounded hypha bearing conidiophores of *Macrosporium solani*. × 650.

FIG. 2. A wounded hypha of *Macrosporium solani* showing the production of conidiophores near the point at which the hypha was cut. × 900.

bear a single spore. If, however, the radiating mycelial strands are severed at the proper stage in the life of the culture, thousands of conidiophores, each bearing a spore, will develop from the cells of these hyphae. The wounding may be accomplished by scraping the surface of the culture with a sterile scalpel or even with a strong platinum needle. The more thoroughly it is done, the greater will be the quantity of spores produced.

Conidiophores arise abundantly near the point at which the mycelium is broken. Sometimes each consecutive cell of the mycelium for a considerable distance produces one or more conidiophores. Such a series of fruiting cells is shown in Fig. 1. At the distal end of some

of these conidiophores may be seen a scar. This indicates the point at which the spore was attacked. The production of conidiophores near a wound is shown in Fig. 2. In Fig. 2 may be seen a portion of a cell that was killed when the hypha was cut. Each of the photomicrographs (Figs. 3 and 4) shows portions of the surface of two different string-bean agar cultures of the early blight fungus. These photographs indicate the abundance of spore production when the mycelium is properly wounded. Many thousands of spores may

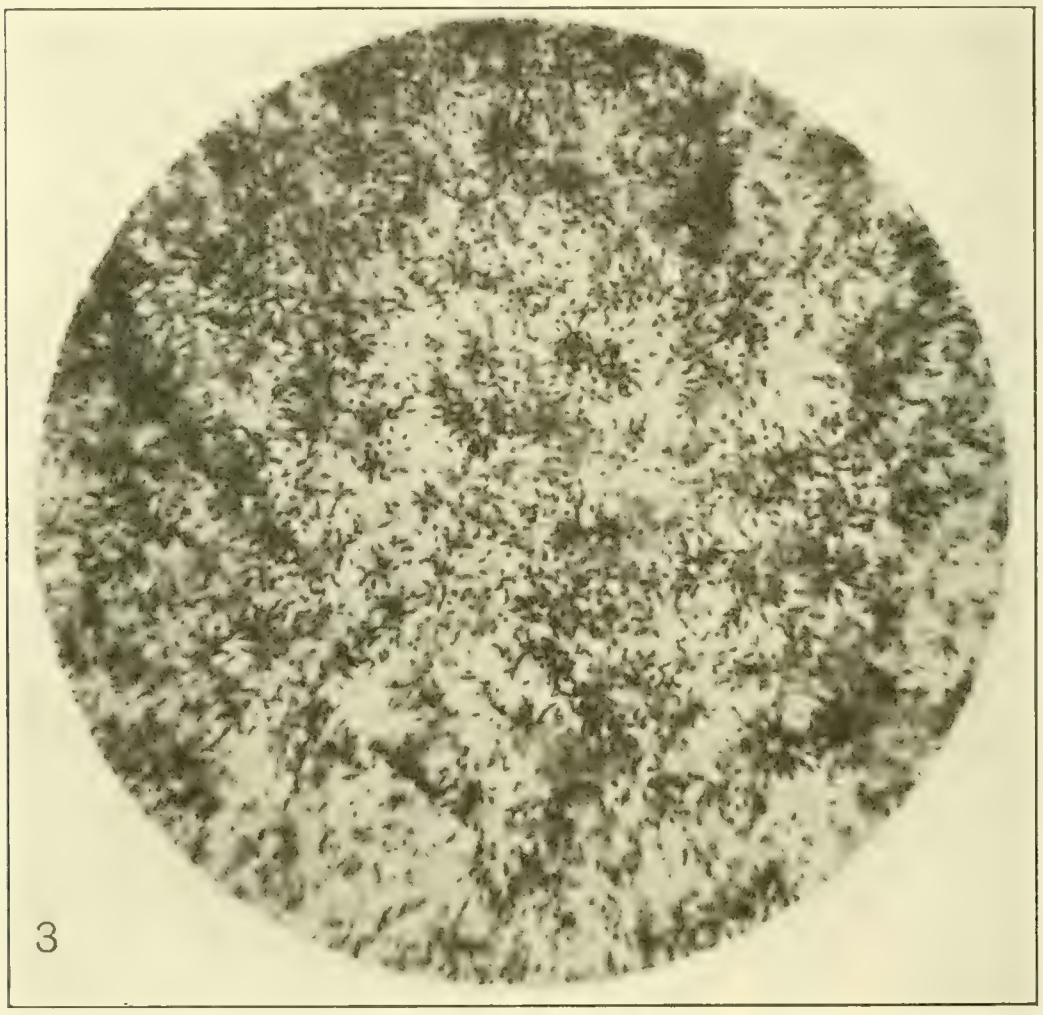



FIG. 3. Fruiting culture of *Macrosporium solani*. This photograph of the surface of a string-bean agar culture shows the abundance of spore production when the mycelium is properly wounded. × 15.

thus be obtained from a single Petri dish culture. Spores produced in this way were sprayed with an atomizer onto potato plants growing in a greenhouse. They produced good infection not only on the older leaves but on young leaves as well.

The method of stimulating spore production by wounding was tested out on each of the single spore strains isolated from the potato

fields of Maine. They all responded in like manner, producing spores in great numbers. The method has also been applied to other Macrosporiums that do not fruit readily in culture. *M. tomato*, Cooke, a parasite of the tomato and *M. daturae*, Fautr., a parasite of the jimson weed, *Datura Stramonium* L. respond in the same way to the wound-stimulus. Although *M. daturae* fruits quite freely without this stimulus, the number of spores produced in any culture can be greatly increased by wounding. *M. tomato* fruits even more sparingly than

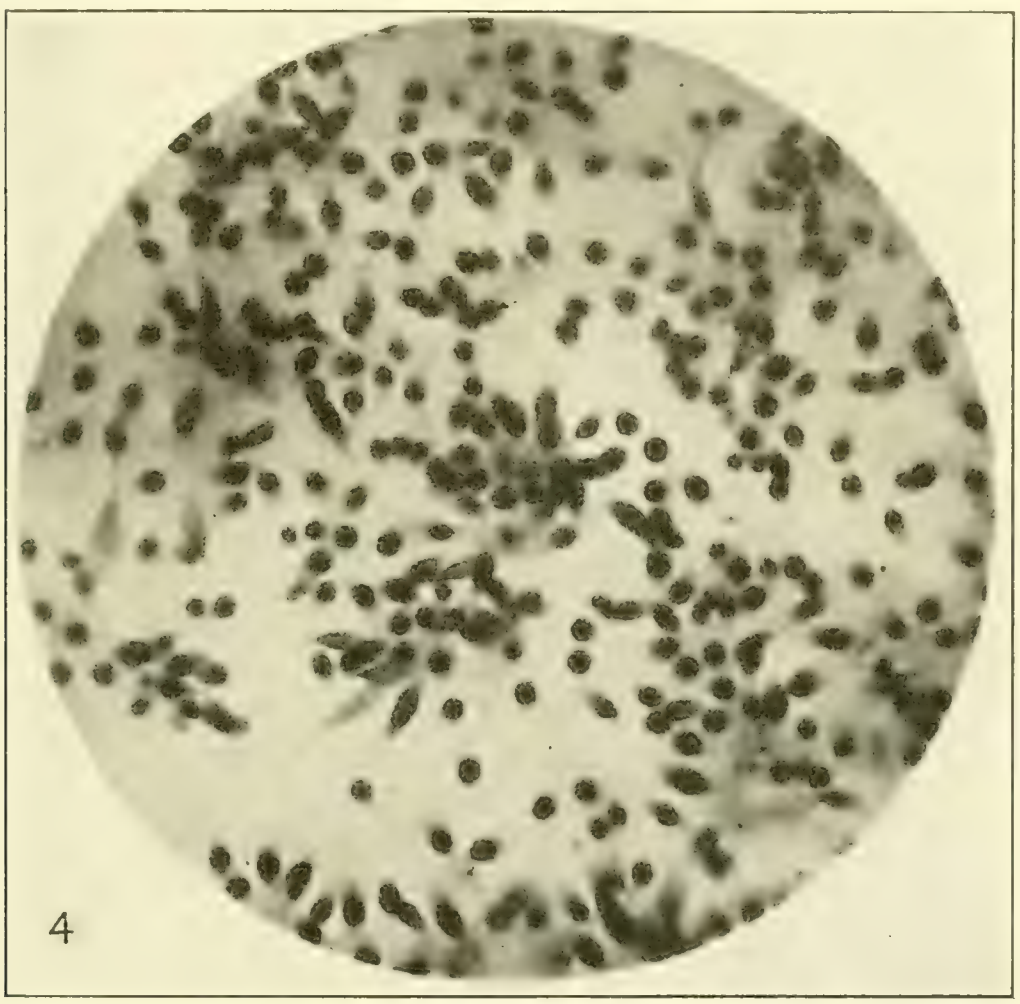



FIG. 4. Fruiting culture of *Macrosporium solani*. This picture shows the spores more highly magnified and indicates their abundance in a wounded string-bean agar culture. × 250.

*M. solani* in unwounded cultures. When thoroughly wounded it bears spores in great numbers.

The abundant sporulation of *M. solani* in culture makes more easy the study of its fruiting stages. The successive steps in the development of conidiophores and spores can easily be observed. The mature conidiophores are always several-celled. They may arise singly or in whorls, as is shown in Fig. 2. The typical conidio-

phore bears a single spore. Successive production of spores on the same conidiophore, such as has been described by Miyabe (7) for *M. parasiticum* Thüm., has not been observed for *M. solani*. Occasionally the spores are borne in chains of two. This may occur quite frequently when the atmosphere above the culture is saturated with water vapor and only a few conidiophores are being produced by a vigorously growing mycelium. It occurs very seldom or not at all in cultures that are sporulating abundantly. The occurrence of spores in chains of two is exceptional for *M. solani*. The writer has never observed longer chains and is inclined to the view that Duggar (1) is correct in leaving this fungus in the genus *Macrosporium* rather than to put it into the closely related genus *Alternaria* as Jones and Grout (5) have done. Duggar's objection that the catenulate method of spore production has not been seen except in artificial culture does not hold, however, for the writer has more than once observed the spores in chains of two on the potato leaf. *M. daturae* when grown under very moist conditions also produces its spores in chains of two. This fungus in rare instances even produces spores in chains of three. Under more normal conditions, however, the spores are always borne singly. As one finds it growing on its host or observes it in pure culture, the catenulate method of spore production is exceptional, and it seems doubtful whether any useful purpose would be served by transferring it to the genus *Alternaria*. The writer has examined many fruiting cultures of the tomato parasite, but has never observed it producing spores in chains even under very moist conditions.

Besides usually producing their spores singly, both the early blight fungus and the jimson-weed fungus show other characteristics which seem to put them with the Macrosporiums. They both possess a coarser mycelium than is usual for the genus *Alternaria*. Their spores are larger and under most conditions are produced in smaller numbers than is common for an *Alternaria*. Moreover, their spores are normally attenuated into a beak similar to that on the spores of other species of *Macrosporium*, such as *M. catalpae*, E. & M., *M. cucumerinum*, E. & E., *M. caudatum*, C. & E., *M. concentricum*, Winter, *M. brassicae*, Berk., *M. porri*, Ellis, and *M. tomato*, Cooke. *M. caricinum*, one of the four species mentioned by Fries (2) at the time he established the genus, bears spores which are, according to his description, attenuated at both ends. No such beaks are to be observed on spores that are borne in chains.

Since *M. solani*, *M. tomato* and *M. daturae* are parasitic on closely related plants, they have by some authors been considered identical. Sorauer (9) seems to have had this notion and Duggar (1) states that *M. solani* "is found not only upon the potato but also upon tomatoes

and upon the jimson-weed (*Datura stramonium*)." By growing the Macrosporiums obtained from these three hosts side by side in pure culture it is easy to observe that they are by no means alike. Not only are they different culturally, but the spores they produce are quite unlike morphologically. The spores of *M. daturae* have an attenuated beak that is very much longer than the beak on the spores of *M. solani* or *M. tomato*. The beak on the spores of *M. tomato* is finer than the beak on the spores of the other two species. The mycelium of *M. tomato* is also finer than the mycelium of the other two forms. The spores of *M. daturae* are larger and the spores of *M. tomato* are smaller than those of *M. solani*. On such media as string-bean agar and glucose agar the three fungi show wide differences. *M. solani* produces a gray felty growth on string-bean agar and usually colors it red. No such color is to be observed in the case of *M. tomato* and *M. daturae* on the same substratum. The growth of *M. solani* on glucose agar is a rusty gray color. Colonies of *M. tomato* and *M. daturae* on this same medium are blue in color. *M. daturae* on many different media produces colonies showing marked zonation, such as is not to be observed with the other two forms. These three parasites are unlike in so many different ways that the writer believes they should be considered separate species, rather than strains of a single species. It is, of course, probable that either fungus may infect more than one host. Sorauer (8) reports that he was able to infect tomato leaves with the *Macrosporium* from the potato. This does not prove, however, that the three hosts as they grow in nature are attacked by one and the same fungus. An examination of the spores of the three fungi when grown side by side in wounded cultures brings evidence that this is not the case.

The method of obtaining abundant sporulation in cultures of *M. solani* here described makes possible more extended infection-experiments than have hitherto been undertaken. It is believed that it will also be of service in any study of the systematic relationships of the genus *Macrosporium*. The principle involved in the response of the early blight fungus to a wound-stimulus is one well known to science. Conditions unfavorable to vegetative growth often lead to fruiting in unprolific plants. The orchardist recognizes this truth when he prunes his trees or feeds them with fertilizers poor in nitrogen compounds.

## BIBLIOGRAPHY

1. **Duggar, B. M.** Fungous Diseases of Plants. Ginn and Co., New York, 1909.
2. **Fries, E.** Syst. Myc. 3: 373. 1829.
3. **Galloway, B. T.** The Macrosporium Potato Disease. Agric. Science 7: 370–382. 1893.

4. **Jones, L. R.** Potato Blights. Vt. Agric. Exp. Sta. R. **9**: 88. 1896.
5. **Jones, L. R. and Grout, A. J.** Notes on Two Species of Alternaria. Bul. Tor. Club **24**: 254–258. 1897.
6. **Kunkel, L. O.** Physical and Chemical Factors Influencing the Toxicity of Inorganic Salts to *Monilia sitophila* (Mont.) Sacc. Bul. Tor. Club **41**: 265–293. 1914.
7. **Miyabe, K.** On the Life History of *Macrosporium parasiticum* Thüm. Ann. Bot. **3**: 1–26. 1889.
8. **Sorauer, P.** Auftreten einer dem amerikanischen "Early Blight" entsprechenden Krankheit an den deutschen Kartoffeln. Zeits. f. Pflkr. **6**: 1–9. 1896.
9. —— Handbuch der Pflanzenkrankheiten. **2**: 455, Berlin, 1908.

# SYNCHRONISM IN PLANT STRUCTURES

JOHN MUIRHEAD MACFARLANE

*University of Pennsylvania*

In all departments of botanical inquiry it is becoming increasingly evident that wide observation and exactness of record are indispensable, if we are to reach wide and exact conclusions as to plant life. So the carefully tabulated experiments of Koelreuter, Gaertner, Herbert, Darwin, Mendel, Vilmorin and others regarding plant crossing during the past century were the appropriate starting points for the more extended and exact results that are now being secured by plant breeders.

The characteristic also of exact and correlated behavior on the part of plant organisms powerfully impressed the writer as he advanced in his studies of parent and hybrid types, from 1889 onward. Not the least striking of his results were those bearing on the relation of plants to environal atmospheric agents or stimuli, such as light, heat and water supply.[1] So alike as regards constitutional vigor and period of blooming as for chemical nature, color, and odor of hybrids, it was concluded that each detail was more or less exactly between that of the parents; "while some vary to a greater or less degree from one or other parent." Impressed, therefore, by such conditions, the writer has observed closely, during a period of twenty-five years, the action of those environal agents which we speak of collectively as climatic conditions, and the reaction of plant parts to these agents, with a view to determining how exactly each plant organism is correlated with its environment. This line of inquiry has received considerable attention during the past seventy-five years, under the term "phytophenology." But the study, as well as the results secured, have been very largely ignored by botanists, or even ridiculed by some as yielding no conclusions of value. We would emphatically assert that few lines of investigation will compare with this if the studies are prosecuted in exact manner, and are planned so as to cover a definite field.

The present communication may be suggestive in connection with future possible developments at such an experimental institution as the Brooklyn Botanic Garden, which has already had so successful a history under its able director.

[1] Gard. Chron. $9^3$: 753. 1891. Trans. Roy. Soc. Edin. **37**: 255. 1892.

Plant variation as due to varying environal stimuli is a phenomenon witnessed everywhere around us. The difference in size and color between similar plants growing in shade and sunshine; the difference in growth and habit between plants exposed to moist rich soil and to light dry sand; the difference in time of leafing, blooming, and fruiting between plants situated at lower and higher levels, are facts that are familiar to all. But the fundamental causes of such differences, as well as the important conclusions to be drawn, have hitherto been too much overlooked. Even the records of leafing, the blooming and fruiting of flowering plants, the shedding of spores by pteridophytic and bryophytic species, or the conjugation period of algoid and fungoid types have often been given in most haphazard, or totally misleading, manner in many of our local floras and manuals.

We desire, therefore, to inquire how far such great seasonal conditions as the above can be reduced to exact limits, and if possible to ascertain what fundamental principles underlie their expression. The writer selects first the blooming period of higher plants as a phenomenon that all can witness and verify to greater or less degree in daily life. Given that some one locality is chosen where a certain number of individuals of a species are exposed to as exactly like environal conditions as possible, it may then be asked how nearly synchronous may the blooming periods be amongst these, and how correctly can we define these for any region. In illustration, the following may be cited from amongst many others that the writer has watched:[2]

Neglecting the wayward skunk-cabbage—that nevertheless can be reduced to system—the first plant to bloom each season is the silver maple. This year (1917) hundreds of trees opened many flowers synchronously on March 11, instead of on the 13th, as is averagely the case. Furthermore, the opening took place about nine to eleven A.M. Favored by bright suns the expansion continued upward along the branches, as is averagely the case, for a period of nine days, and by this time the earliest flowers were beginning to push out their green fruits. If we compare now the same trees for previous years it may be said that during 1912, and as a result of continued snows and frosts, the unfolding occurred with equal abundance and exactness on March 17. In 1913 a remarkable record was made. The weeks of fall weather during 1912 were balmy and mild, and even at times warm. As a result many heat units over the average were absorbed by the trees and caused precocious though unobserved preparation for spring unfolding in 1913. And here we would emphasize again, contrary to views previously expressed by many, that record must be kept of environal conditions continuously throughout years, if true

[2] The results recorded are given for West Philadelphia unless otherwise stated.

results are to be secured as to the action of environmental agents. To attempt to start the record from such an artificial period as the first of any year is to set an arbitrary limit to the continuity of changes and activity in vegetation.

The short-lived snow and slight frosts of late November started the apparently needful winter maturation of tissues, and this was followed by an almost continuous series of genial days until the third week of January. So on the morning of January 19 abundant first flowers expanded on all observed trees, but a cold wave on the 21st split the flowering period in half, and only on March 2, with the advent of a bright day and warm sun did the opening again proceed until March 10. This striking result had not been paralleled through a previous period of at least thirty-five years. As a contrast, in 1914 expansion occurred only on March 16, owing to the frosts and late temperatures occurring throughout February and on to March 15. In the neighborhood of Wayne, Pa., with an elevation of 475 feet, with greater exposure to cold winds and less influenced by the heat of a great city, the opening did not take place until the 22d of March. Records like the above that extend over more than twenty years would suggest that floral expansion is not a somewhat haphazard and irregular event, but is rather an exact reaction of an organism to definite and cumulated environal actions or stimuli. If such be true, we should expect it to extend probably throughout flowering plants as a group. Partial proof is subjoined.

The red or swamp maple (*Acer rubrum*) each year succeeds the silver species in blooming at an average interval of twelve days. This year, eleven trees, observed in like locality, all opened on the morning of March 26, while the climax of blooming was reached on the 4th of April.

According to the valuable statistics secured by Dr. Mackay and his committee of observers, it may be instructive here to point out that the same species in Nova Scotia has expanded averagely on May 5, or 41 days later than in the Philadelphia region.

The white poplar (*Populus alba*) is of exceptional interest from the standpoint of the present communication. Staminate catkins annually mature, and lengthen synchronously, amid like environment on a definite day, and the shedding of abundant pollen proceeds for one or at most two days. Thereafter the catkins soon shrivel and within a week have mostly fallen. The average blooming date is April 7, but this year, stimulated by the warmth of mid-March days the tassels suddenly lengthened on March 28. Pollen was completely shed by the 29th, and sidewalks over wide areas were covered with fallen tassels by the 2d of April. But though a comparatively rare

tree, the pistillate plant of this dioecious species has been proved to mature its stigmas synchronously with the shedding of pollen from the staminate trees. The yearly variations from the above dates vary according to environal—mainly heat—stimuli. Thus in 1912, after a cold February and early March, succeeding favorable days caused complete pollen dispersal on the 27th and in part on the 28th. During the precocious springtime of 1913, the flowering occurred suddenly and uniformly on the morning of March 18, while in the succeeding year like expansion took place on March 31. The Carolina poplar (*Populus deltoides*) is like the last species specially abundant in the staminate trees, rare in the pistillate ones. Its average blooming period is April 16. In 1913 its behavior was arresting in the sudden and exact procedure shown. Here, these trees under similar environment lengthened their catkins fully and started to disperse abundant pollen on March 24, between 9 and 10 A.M. of a bright warm day. The young catkins were almost emptied by 5 P.M., only a few of the smaller terminal flowers still retaining a quantity. By next day, scant remnants could alone be secured. But on that day four trees which grew on wind-swept and shaded street corners were found only beginning to dehisce.

In 1914, owing to prolonged cool periods and warmer ones alternating, blooming occurred on April 6. Many catkins matured only on the 7th. During the present year, the action and reaction of environal energy and of organismal tissue have been most suggestive. For stimulated by the bright warm suns of March 31 and April 1 some catkins lengthened gradually during these and succeeding days, and began to discharge pollen extensively on April 4. But rather low temperatures on that day and those succeeding, accompanied often by rain, prolonged reaction fitfully until the 10th of the month. So we learn from such statistics, that have frequently been verified for the above, as well as for other species, that if a sufficient environal stimulus act quickly and continuously, an extensive synchronous blossoming may ensue, that is completed within a few hours each year. On the other hand, if temperature units be more gradually expended, and specially if such be combined with wetting conditions that prevent establishment of tissue tension in anthers, pollen discharge may be prolonged over a considerable period.

The alder (*Alnus incana*) that averagely lengthens and opens its catkins on March 24, and that shows crimson papillose stigmatic surfaces in exactly synchronous manner, was in like state on the 25th, but in 1913, March 12 was the date. Pollen dispersal is usually completely effected in three or at most four days, this lengthened period being due to differences in position and so in time maturation of the catkins on each twig.

The above are all shrubby or arborescent forms, and so are more directly subject to changes of temperature than are species that perennate by subterranean parts. The energizing factors are less complex in the former; while in the latter, warmth, moisture, porosity and chemical composition of the soil, become highly important governing factors. So the digestion and transfer of the reserve foods in rhizomes, corms and bulbs is effected more gradually and the flowering period is usually more prolonged, though the exactly synchronous unfolding of the first blooms is as striking as in any of the shrubs or trees. Of our three commonest spring flowers, *Hepatica triloba*, *Sanguinaria canadensis* and *Claytonia virginiana*, the two first averagely appear in bloom on April 9, and open successive flowers for a period of 18 days in *Hepatica*, 10 to 12 days in *Sanguinaria* and about 25 days in *Claytonia*. *Claytonia* appears in bloom on April 12, averagely. But in 1913, our woods showed a sudden unfolding for the first two on March 18 and of the last on March 20 or 21.

Another herbaceous plant deserves special notice here as illustrating an interesting phase in synchrony, namely, the dandelion. Like the English daisy (*Bellis perennis*), this is a hardy plant which retains wintergreen leaves and shelters amid close grassy sod. So very slight changes of temperature in winter will cause both of these to unfold their earliest flower-heads in apparently regular manner, specially if growing in sheltered sunny places. But such by no means represents the first exact growth period for the season, which for the dandelion occurs averagely on April 23. Then, instead of the scant or occasional heads of earlier date, our lawns show a sudden yellow coloring by 9 A.M. that is continued for almost a month thereafter, as successive heads expand and as the florets in each successively open. During 1913, the behavior was noteworthy. For lawns were abundantly yellowed over from January 16 to 20. But all suddenly closed and were destroyed by frosts that succeeded from January 21 to March 2. Then came a warm stimulating March, with the result that from the 15th of the month onward dandelions were abundant.

In connection with his graduate class on the Gymnospermia, the writer became interested from 1898 onward in the behavior of the Japanese ginkgo tree (*G. biloba*), at first only with the aim of securing appropriate material, but as the years passed the phenological relation became of equal interest. Two large staminate trees grow near the historic old Hamilton Mansion, adjoining the University Botanic Garden. These suddenly and synchronously lengthened their catkins in 1898 on the morning of May 2, and when visited on the succeeding day few were still polleniferous. This suggested to the writer a closer study of the subject from the standpoint of individual and species

behavior. During the previous two years he had secured scant supplies of good seeds from a large pistillate tree fronting the old Jones Home at 65th and Callowhill Sts. Throughout the summer of 1898 he examined it from time to time, and noted that the seeds matured wholly on the southeast side, though no staminate tree was then known to exist for miles around. In the succeeding spring the two staminate trees matured between 9 and 10 A.M. on May 5, and by the 6th were equally free of pollen as before. But the possible synchronous relation of these to the pistillate tree was now determined. For, accompanied by one of his students and laden with staminate branches, a visit to the latter tree was made on the 5th. A ladder was secured and examination of the small green ovules on the branches clearly revealed that each was exuding a shining viscous droplet for pollen entanglement. The staminate branches were hung over the western side of the tree and then shaken. As summer advanced the abundant maturing ovules alike supplied wealth of material for study, and by their structure showed that perfect pollination had been effected. Continued study of the above trees in succeeding years showed that synchronous maturation and rapid pollen discharge annually took place as early as April 20 in 1913 and as late as May 22 in 1904, according to the stimulating amount of heat units, of rain condition and of soil moisture. In time also as the above statistics became known, the writer learned of staminate trees on the grounds of Girard College, and Laurel Hill Cemetery, which doubtless had contributed pollen to the pistillate tree, widely removed from them, during previous years.

The peach (*Prunus persica*) deserves attention as being an introduced woody plant, that bears attractive flowers and valuable economic fruit. Trees under like environment open averagely on April 22 and then in considerable numbers. Climax of blooming is reached five days thereafter and within another four days the flowers have all fallen. But in 1913 a sudden wealth of bloom appeared on April 1. It need scarcely be added here that a synchronous activity amongst pollinating bees was a feature of the event.

The common field daisy, that like the dandelion and English daisy, are all European and introduced weeds, differs markedly nevertheless from the other two in that it shows no unseasonable flowers throughout the winter months and does not even unfold as a harbinger of spring. For averagely a sudden wealth of flower heads expands on May 24, and for a month thereafter added heads appear in what may be—did we only know accurately enough—regulated succession.

Almost exactly a month after the last, the first flowers of the introduced moth mullen (*Verbascum blattaria*) come into bloom on June

26, and in wonderfully exact and graded succession, with definite time interval between each, later flowers open along the elongating axis. But just three days before, or on June 23, the central flowers of the cymes on our common Indian bean (*Catalpa bignonioides*) expand, and for about 16 days thereafter successive blooms open in exact ratio, if weather conditions are favorable. But a decided retardation may occur, if cold winds and wetting rains interfere.

We would draw attention now to some cases of synchrony in floral parts. From the time of Linnaeus onward descriptions of floral clocks have been frequent, and no matter what value we attach to such, the very device points to a surprisingly exact time during the twenty-four hours when the blooms of each species open. But the maturation and opening of each flower, as well as the behavior of such parts as the stamens and styles of it, may vary according to the degree of thermic energy, or lumic energy, or both that act on these. Such variation seems to explain apparently contradictory results that have been recorded by different botanists. Thus Kerner's attractive statements[3] regarding *Silene nutans* and its successive maturation of one row of stamens in each flower, on one evening, of a second row on a succeeding evening, and of the styles on the third, have called forth adverse comment along with the statement that no such exact succession occurs. But first about twelve years ago along the Trafoi Ravine in the Tirol, and nearly seven years ago by Morgarten Field in Switzerland, the writer was able to prove that both statements might apply according to environal conditions. For when the days and nights in August are warm, with clear sky overhead, the exact succession noted by Kerner can readily be traced. But if the days, and even more the nights, be cold, raw and at times accompanied by rains, then a nearly simultaneous maturation of all ten stamens and at times even of the styles may occur.

By careful observation, however, during warm dry days we were able to determine an even more exact and synchronous behavior of the ten stamens than that noted above. For on the first evening from about 6 to 7.30 the anthers of the earlier 5 stamens matured in circular succession with a clear time interval between each, and then were ready to scatter pollen; while on the succeeding evening, the second five ripened similarly. Such again calls to mind the time period shown in maturation of the five anthers on the stamens of the giant cow parsnip (*Heracleum lanatum*). It was found even that the dropping of the anthers in *Silene* mentioned by Kerner takes place not together, or irregularly, but in correlated succession if environal stimuli are favor-

[3] Nat. Hist. of Pl. 2, p. 154.

able. But here again this is duplicated by *Heracleum* and other Umbellifers, as well as by many Araliads.

The writer can never forget his first knowledge obtained for the almost exactly synchronous floral expansion in *Oenothera grandiflora.* Two enthusiastic botanical lady friends had cultivated many of these handsome plants along with numerous other species nearly twenty-three years ago. He was asked to pay a visit about 7 P.M. on a mid-July evening. Chairs were set out amongst a group of the Oenotheras and he was asked to watch and listen. From 7.15 to 7.50 a constant succession of "pfuffs" was heard, that indicated the bursting of the sepals and unfolding of the petals, which rapidly took place before one's eye. From the condition where scarcely a flower was open to begin with, to that seen at 7.50 the change was striking, for now the plants were gay with large expanded blossoms. Six years afterward the writer was carried by train from Botzen to Meran in the Tirol toward 7 P.M. and running for miles by the banks of the Adige River he witnessed the same synchronous series of events for plants of *Oenothera* that had been introduced there.

In connection with genetical studies increasing attention has been paid during the past fifteen years to the behavior of varieties and hybrids. But extremely little has been published as to the relative period of flowering, fruiting or like phenological conditions for each parent and for the hybrid. But a very wide field for exact observation is here awaiting study. The writer has drawn attention to some results and has since accumulated others. Thus, the relative production or not in the wild state of hybrid Sarracenias is almost wholly determined by the synchronous or asynchronous relation of the flowers. So the scarcity of wild hybrids of *S. rubra* with other species is in part due to difference in locality, but in large measure to later blooming period of that species. Under cultivation by placing plants in greenhouses of different temperatures a synchronous blooming can be effected, and such striking hybrids as *S. Popei* and *S. Chelsonii* represent the progeny. In such cases then an exact expenditure or retardation of definite heat units effects a synchrony that in their natural environment does not exist. The practical application of such methods in the prosecution of hybridization experiments will ensure success where failure might otherwise result.

The writer has watched with interest the phenological behavior of a wild hybrid between *Myrica cerifera* and *M. carolinensis,* that his former graduate student, Dr. Youngken, has described under the name of *M. Macfarlanei.* The first of these is a narrow-leaved evergreen shrub or low tree, that has its northern limit in New Jersey round the mouth of the Great Egg Harbor River, and there the rather

dull deep-green leaves are quite green even in mid-April of each succeeding year alongside other and deciduous vegetation. These evergreen leaves defoliate in May or early June after the young leaves and flowers have well expanded. The species moreover invariably occurs only where facing sea breezes or along the edges of ocean inlets, as observed along a stretch of the New Jersey coast-line from the mouth of the Great Egg Harbor River to Cape May Point, and is invariably a swamp-loving plant.

*Myrica carolinensis*—the common Waxberry or Bayberry—is a deciduous species of much wider range and greater hardihood, which drops its elliptic obovate shiny leaves by the end of November, at latest, and whose bare twigs throughout the winter show only the small protruding staminate catkins on one plant and the even smaller pistillate buds on another. The species occurs often many miles removed from the influence of ocean winds or brackish water and nearly always in dry sandy soil.

The hybrid—*M. Macfarlanei*—is of semi-evergreen habit. It grows frequently interspersed with both parents along the area of the New Jersey coast already named and doubtless will be recognized southward to Florida. Its lanceolate leaves of rather shining aspect remain green to the end of March, or only become in part brown and fall during April. More extensive and exact studies made as to the occasional retention of leaves on low young shoots of *M. carolinensis* into mid-winter and the retention of the evergreen leaves on *M. cerifera* to an even later date than the writer has indicated, may yet make our knowledge much more perfect regarding this striking hybrid and the possible synchrony of floral events, as well as leaf duration on individuals of the parent and of the hybrid. It might be added that the hybrid inhabits soil areas which are fairly intermediate between the swamps of the one species and the dry sandy soil of the other.

If we consider now germination of seeds, equally suggestive synchronous procedure is observed. Only two, amongst many studied, need be mentioned as having recently been closely examined side by side with each other. The seeds of the little annual *Floerkea proserpinacoides* germinated this year in immense quantities over several moist shrubby valleys on March 17. The radicle had protruded and the cotyledons had become swollen on March 25, the first or trifoliate leaf was uniformly mature on April 7 and the second leaf was unfolding by April 11. In contrast, subterranean seeds of *Amphicarpaea monoica* alongside the above, were still dormant on April 11, but on April 14 many had simultaneously begun to germinate.

Moreover, but in line with all of the above, the annual transformations that occur in our woodlands in spring and throughout

summer, when compared from year to year, are as exact in relation to time and energy expenditure as are the flowering periods. Thus, if we compare the vegetative growth of the Yellow Adder's Tongue during 1913 with that of the present year the tips of the leaves were simultaneously emerging from the ground over wide areas of a valley on March 27, while this year they appeared on the 11th of April. In both cases these leaves were $2\frac{1}{2}$ inches high 3 days thereafter, and so comparatively suddenly transformed wide woodland areas from a bare unclothed aspect into rich showy brown-green verdure.

If we consider now a few naked eye details that depend on definite histological changes, it may be said that botanists are aware that for any given species of shrub or tree a fairly definite period arrives when easing and separation of the epidermis along the stem is effected, after cork formation has replaced it functionally. Some species show this change in the latter part of the first year, many in the early part of the second, while others may be delayed until the following autumn or even later. A more pronounced though related occurrence is seen annually in the oriental plane. The extensive flakes of old dull-gray cork start to separate synchronously on the average about June 28 and so reveal the white younger cork underneath with increasing effect during the next few days, but variation as to date of this event may occur from year to year according to environal stimuli. Opportunity has twice occurred for comparing this with the behavior of the same species round Kew Gardens, England, and there a like change starts on July 29. This comparative result agrees closely with other data obtained as to floral maturation.

Closely related again to the above studies is one that has scarcely been touched in this country, but which has been investigated by Hoffmann-Ihne in their observations at Giessen. This is an exact comparison of flowering periods according to longitude and latitude, particularly the former. Exceptional facilities exist for the prosecution of such an inquiry in this country, for were thirty or forty observational stations established under competent workers, and the whole correlated at a central office, valuable results would accrue after a period of ten to twelve years. A feature of interest here is that a considerable number of plants of the eastern seaboard extend their range from central or northern Florida to Newfoundland or even Labrador. One of these which the writer has shortly referred to elsewhere[4] is our native pitcher plant (*Sarracenia purpurea*). In northern Florida, as for example round Ponce de Leon, it starts to bloom in the last week of March and continues until April 10. In the Charleston region, as at Summerville, it is averagely five days later;

[4] Engler's Pflanzenreich, vol. 4 (1908), p. 23.

round Wilmington, N. C., it begins on April 18; in central New Jersey, it opens on the 20th of May; in northern New York and Minnesota it blooms from the 14th to the 26th of June. In eastern central Maine the period is from the 8th to the 20th of July, while in Labrador—the northern limit of the species—it finishes in mid-August. Thus a period of fully five months is represented, and a longitudinal area of about 2,000 miles is covered, in the floral maturation of this one species. In connection with such records, and probably due to the more gradual and even expenditure of environal heat stimuli is the much more extended floral period of species in the cool north than in the warm south. Thus while the double Crimson Rambler and Dorothy Perkins roses show floral attractiveness from June 10 to June 25 averagely round Philadelphia, on eastern Mt. Desert the period extends from July 15 to August 30.

Were the valuable records, inaugurated in 1892 for Canada by Mackay, to be linked up with like records from widely distributed stations in this country, and were all to be correlated with temperature or thermotactic and moisture or hydrotactic stimuli, as has in part been done by the Canadian observers, a most valuable foundation for the establishment of facts regarding the action of definite environal stimuli would be made.

A very wide field for exact study, still left practically untouched, is the observation and recording of sporangial ripening and spore dissemination in pteridophytic and bryophytic genera and species. One or two references need only be made here.

For years the writer was puzzled to know when spore-dissemination took place in the sensitive fern (*Onoclea sensibilis*). Though the green sporophylls shot up in late July and became greenish-brown in autumn, opening of the modified pinnae and dissemination of spores clearly did not take place before winter. Passing through a swampy patch of this on March 24 of five years ago his clothes became browned over with the shed product. Subsequent study has shown that this event occurs averagely on March 25, and in any one patch or locality with surprising synchronous exactness. Like observations should be made for *Onoclea Struthiopteris*.

The sudden and simultaneous elongation of the sporophores and the subsequent rupture of the sporangia in such hepatics as *Pellia endiviaefolia* is familiar to all in mid-April, but we still lack exact day and hour records through succeeding years for the entire group of scale mosses.

The predicable manner in which, when fresh horse manure is placed under bell jars in the now familiar laboratory experiment with *Pilobolus*, an abundant crop of the black sporangia is shot forth on a

morning after a definite number of days of growth, is as indicative for that fungus as is the previous growth of *Mucor* on the same medium, within a shorter period.

What conclusions, it may now be asked, can be drawn from data such as the few above given?

Time, space, energy and matter are the four great interrelated phenomena of the world, as of the universe generally. Not a few physicists now question the existence of the last of these, but inert and mobile ether particles as focal centers and pathways for "tubes of energy" seem to be helpful—even necessary requirements. For by their gradual aggregation under increasing condensations of energy we can explain the origin of the elements, and equally the compounds of these. But the fundamentally important consideration is how, when, and to what extent in given times, do definite tubes of energy distribute themselves.

In the foregoing pages a set of simple facts has been recorded that any average observer might accumulate. But the real value of many of them has been overlooked, because we have not fully realized the significance of the causes that bring them about. For in the past we have largely viewed biological phenomena as static or semistatic exhibitions of so much material substance. But we have in great measure failed to realize that matter as such is physically passive or inert, and that the fundamental moving, transforming, upbuilding, and disintegrating agency in all of the above phenomena of phytophenology consists in definite expenditures of definite amounts of energy along definite material pathways. Or to use Faraday's phrase as applied to inorganic changes, we are dealing with "tubes of energy" that are distributed along definite material pathways, at stated climatic periods, and that are marvelously exact for any one species, or any one organ of a species.

In the process these tubes of energy are exactly expended so as to stimulate the inert material particles to take up water, to digest or metabolize reserve products, to convey the metabolized products to definite cells or cell walls, to build these up into new material linkages or combinations, and in the process to effect growth of leaves, opening of flowers, dehiscence of anthers or of sporangia, maturation of ovules and extrusion therefrom or from some accessory part at exactly appropriate time of viscous entangling secretions that strand the pollen grains, and that in time aid in the germination of these; or again that start like initial changes in dormant seeds, once so many units of heat, moisture, and oxygen have cumulated as summated tubes of energy after a definite period of time; or that develop new cells or transform older ones, so as to effect shedding of epidermis or

peeling of bark on twigs of trees and shrubs at exact time; or that effect passage of food material from elaborating to storing centers, and from the latter in turn to young developing organs.

Even such irregular and delayed occurrences as already noted regarding the flowering during the present season of the Carolina poplar, or during 1913 of the silver maple (*A. saccharinum*) represent fitful and prolonged results due to weakened or cancelled tubes of energy-stimulation expended over an extended period, as compared with the normal succession of events that may be consummated within a few hours on a definite day or days. So we might summarize as follows our conclusions drawn from study of phenological and related events:

1. For any one locality, under like environal surroundings, the average annual period of seed-germination, leaf-formation or unfolding, first period of blooming, dissemination of pollen, and other responses by flowering plants, seem to be synchronous often to a day, and even to certain hours of one day.

2. In monoecious and dioecious flowering plants, under like environment, all evidence tends to indicate that maturation of complimental floral organs is effected in exactly synchronous relation, and so abundant pollination usually ensues.

3. A like principle apparently applies to the maturation and dispersal of spores and organs of conjugation.

4. The behavior of plant hybrids strongly suggests that each is a blended combination of parental characters as to period of leafing and defoliation, of blooming and pollination, capacity for climatic resistance and other phenomena. So each shows synchronous behavior in its organs, that is a mean—all environal factors being considered—between those of the parents.

5. The principle, advocated by the writer for the past six years, of environal action and organismal reaction, seems to hold true in the organic as in the inorganic world, and only needs to be amplified and demonstrated by increasingly accurate and extended observations on plants over wide areas.

6. In the evolution of all plants and of all plant parts, the fundamental and important consideration is the exact distribution of lines or "tubes of energy" (Faraday) along otherwise inert material pathways; the lines of inflowing energy constituting stimulation *actions*, the lines of outflowing energy constituting *reactions* on the part of the organism.

7. Such actions and reactions show an optimum, as well as a maximum and minimum of interrelation. The optimum for the individuals of each species, and for the organs of this, under like environment, often constitutes a phase-relation that recalls like phase-relations amongst inorganic bodies.

8. The material constituents of each plant organism—in themselves inert—constitute the gauge or measure by which tubes of inflowing or stimulant energy, and outflowing or reaction energy can best be estimated. The structure of all plant organisms, therefore, is a cumulated expression of the continued flow of definite tubes of energy, and the resultant placing, in definite and orderly manner, of otherwise inert material particles, when moved by such streams of energy.

# THE PROBLEM OF THE IMPORTED PLANT DISEASE AS ILLUSTRATED BY THE WHITE PINE BLISTER RUST

HAVEN METCALF

*Bureau of Plant Industry, U. S. Department of Agriculture*

Within the last few weeks the civilized world has stood aghast at the stories told by survivors of the devastation wrought by the German army in its retreat from Northern France. Particularly *schrecklich* are the stories and pictures showing the rows of fruit trees cut down without being utilized for fuel, apparently with no purpose other than wanton destructiveness. But if we pause to think we realize that the Germans did not do the worst that they could have done. The fruit trees are cut down, to be sure, but others can be planted in their places. We may expect in future years to see the old orchards completely rehabilitated. But let us suppose that instead of simply cutting down trees in Europe, any enemy should see fit to leave them standing but thoroughly incoulated with diseases which would not only destroy the present stand of trees but would prevent their future profitable culture in the same territory. To take an extreme example, suppose that some malignant person or nation should see fit to introduce into Europe from America, the Colorado beetle, the pear blight, the chestnut bark disease, and the citrus canker. Surely the world would stand aghast at this if its significance was generally realized, because this would not only destroy or seriously damage the present generation of plants concerned but would tax the agricultural resources of Europe with a perpetual burden. No more fiendish blow to the economic resources of a country could be imagined. Yet this is exactly what we have allowed foreign nations to do to us without resistance, through our lax laws regarding the importation of live plants, or rather through our virtual absence of laws on this subject. We have permitted our country to be invaded by not one but many—perhaps hundreds—of diseases and pests which constitute a permanent tax upon our agricultural and forest resources, and up to the present time we have made scarcely any serious effort to prevent further invasion.

The Bureau of Entomology has issued a large bulletin entitled "A Manual of Dangerous Insects Likely to be Introduced in the United States Through Importations." I understand that this

bulletin lists about 2,700 such insects and that it also lists 130 important insects which have already been introduced into the United States. If a thorough canvass was made of foreign literature I have no doubt that as many plant diseases could be located and described which are likely to be introduced into the United States, and many of them produce as much devastation as the chestnut bark disease, the asparagus rust, the potato blight, the citrus canker, or many other diseases that could be named. Unfortunately, we have at present no corresponding manual of plant diseases that are likely to be introduced into the United States.

There has never been a time when the danger from imported diseases and pests was so great as now. Commerce in living plants has in recent years extended to the ends of the earth. I have in mind one nursery company which makes a specialty of novelties from the Orient. This company is distributing throughout the United States plant material from all parts of Asia. Most of the things that they bring in are woody plants, many related to our American species, and on account of our comparative ignorance of the botany and zoology of the Orient we have no idea what diseases and pests are coming in with Oriental material. The San Jose scale, the chestnut blight, and the citrus canker are only a part of those that have come in already. Not only is commerce being carried on with countries from which hitherto there have been only scattering importations of live plant material, but material brought in now is much more miscellaneous and reaches this country in a much shorter time. There is at present a limited amount of port inspection but too limited to be efficient and the canker diseases and many insects can not be detected by any sort of inspection. The roots of plants imported with earth about them can not even be inspected and such plants constitute a particularly dangerous class of imported material.

The white pine blister rust (caused by *Cronartium ribicola* Fischer), which I am here considering as a fairly typical example of the imported disease, has long been known in Europe. It apparently originated in Asia and spread in Europe upon *Pinus cembra*. When the American white pine (*Pinus strobus*) was introduced into Europe it proved subject to the disease. The first authenticated record of importation of white pine transplants from Europe to the United States dates back only to 1899. From that time until prohibited by law such importation was extensive, as such transplants could be imported more cheaply than they could be grown in America. There was, furthermore, a prevalent belief among nurserymen that white pine seedlings could not be successfully grown in America, a belief which has since been proved erroneous.

The disease was first positively reported in America in 1906, on *Ribes*. No notice appears to have been taken of this warning. In 1909 enormous quantities of diseased pine nursery stock were imported. Probably 95 percent of all diseased seedlings imported into America came from a single nursery, that of J. Hein's Söhne at Halstenbek, Germany. This nursery, on account of its use of *Ribes* hedges, was curiously well adapted to distribute the disease. In June, 1909, a meeting was held in New York City of pathologists and foresters of New England and the Middle Atlantic States, at which a further alarm was definitely sounded. With one exception, all states represented discouraged importation of white pine from that time, but commercial nurseries continued to import extensively until such importation was made illegal in 1912. Unfortunately, no studies of the white pine blister rust have been made in Europe by any American investigator, but if European accounts of the behavior of the disease can be trusted, the disease has apparently spread more rapidly and with greater virulence in New England than it did in Europe. Probably the new climatic and host relations are more favorable to the disease. In any case the problem of invasion presented by this disease makes an interesting study. The black currants, especially the cultivated varieties, are particularly subject to the disease and in areas of scattering infection are reliable indicators of its presence. It was hoped by many that the disease might prove to be only one of nursery stock and reproduction, but at several points in New England, New York and Minnesota, it is attacking large trees. On *Ribes* the disease was in 1916 generally prevalent throughout New England, which means that the actual infection of pine is much more general than is obvious at present. Inspection of nursery stock for blister rust is largely futile since the rust often incubates in pine tissue for many years before becoming apparent by distorting growth or fruiting. According to Ravn this incubation period may be as long as twenty years.

The control of the disease in America presents three separate problems:

First. West of the Mississippi River. In this territory the disease is not known to occur, but undoubtedly has been shipped in on nursery stock of either pine or *Ribes*. If it has not been carried into this territory on nursery stock already, there is little possibility of its ever getting in by natural means. During the coming season an extensive survey will be made of these states to determine whether the disease is or is not present. If the disease should once become established under western forest conditions, its control would be hopeless. All 5-needle pines of this area, including the very valuable sugar pine and

western white pine, are subject to the disease, and wild *Ribes* of many species are abundant. No species or variety of *Ribes* yet tested is immune to the disease.

Second. From the Mississippi River to the Hudson River. There is an area about 30 miles square in Minnesota and Wisconsin northwest of St. Paul which is now known to be heavily infected. Probably more infection will be found in Minnesota. In Michigan, Indiana, Ohio, Pennsylvania, and New Jersey the disease has been found in a few nurseries and plantations and is believed to have been eradicated at these points. In New York west of the Hudson River it has been found in both nurseries and plantations and largely eradicated, but on account of the extensive planting of pine nursery stock in the Adirondacks heavy infections are to be anticipated there. In general, the commercial currant-growing sections, such as the region from Rochester to Buffalo, may be expected to soon show general infection. In Canada the Niagara Peninsula is already generally infected, and at least scattering infections occur elsewhere in Ontario. This infection is of course a serious menace to Michigan.

Third. East of the Hudson River. Here infection is so general that the only hope of successful growing of white pine in the future lies in the elimination of the alternate host of the disease; namely, *Ribes*. Whether such elimination can be made at a sufficiently low cost to be profitable remains to be seen. Probably in localities where *Ribes* occur sparsely, as in Connecticut and Rhode Island, a great deal can be accomplished. However, in many sections of rough country, where wild *Ribes* are too prevalent to be profitably eradicated, white pine growing may be expected to become impracticable. Throughout any section where the blister rust becomes prevalent, the effect is to make the white pine a cultivated plant; that is, it can not be profitably grown, or perhaps not grown at all, unless the ground is kept free from *Ribes* by artificial means.

There are certain difficulties which stand in the way of any general campaign of disease control which involves wholesale eradication of diseased and susceptible plants. It remains to be seen whether these difficulties are or are not insurmountable.

1. There is in the United States no central authority to act in any matter involving destruction of diseased plant material or precautionary destruction of that which is not diseased. Whatever destruction is undertaken must be undertaken in each state under the separate legal authority of that state. The state laws are not uniform. In some states they are adequate and well supported by public sentiment, in others they are wholly inadequate and apply only to special cases. In general there are few states in which the laws are

not so flexible but that a single unconvinced or cantankerous individual can nullify the work of an entire community.

2. The laws governing plant eradication are administered in different states by various officers, but in the majority of states by the state nursery inspector, who is nearly always an entomologist. Some of these entomologists are thoroughly trained in plant diseases and fully appreciate their significance. Others have little knowledge of them and less interest. All of these officers are overworked already. In spite of the activities of plant pathologists, there is profound popular ignorance as to the nature and significance of plant diseases and especially of the dangerous qualities of newly imported diseases. The general public is far better informed regarding "bugs" than regarding fungi and as a matter of fact the average man considers that plant diseases are caused by "bugs."

3. In the case of the blister rust, there is no single interest or centralized affiliation of interests whose securities are menaced by the disease. The white pine industry is diffused over a wide territory and in the hands of many separate individuals and organizations. What is everybody's business is likely to be nobody's business. If the white pine industry, like the redwood industry, for example, or like the citrus industry, were in the hands of a few people or constituted the dominant business in certain areas, the control of the disease would be much simpler.

4. Up to the present time there has been no adequate quarantine against the disease, either state or national. This difficulty, however, will shortly cease to exist as many states have recently declared quarantines and on June 1, possibly earlier, an adequate national quarantine will go into effect.

5. Finally, we have a very serious consideration which is applicable to all undertakings at the present time. The nation is at war. The young men who would ordinarily be employed in an eradication campaign will soon be drawn away into military work or into the various lines of industry which bear directly upon the conduct of the war. The majority of the persons employed in this particular eradication campaign can only be employed from the middle of April to the first of November. Necessarily, men will be loath to accept such temporary employment when they can in other lines secure permanent employment at an equally high or higher wage. In any case, the work if successfully prosecuted or indeed if prosecuted at all will involve much larger expenditures for wages than in normal times.

What then is the outlook for the control of the white pine blister rust? It may be expected that the future course of the disease will be much like that of the gypsy and browntail moths; that is, the dis-

ease can be controlled for a long period of years in those localities where infection is not general but in areas of general infection the control will be only local and the efficiency of this local control will largely depend upon whether the white pine as a crop is of sufficient value to sustain the added expense of the eradication of *Ribes*. It is to be hoped that any infections found west of the Mississippi River will be scattering and small, for, as has already been stated, if the disease once becomes established under western forest conditions its control even on a local basis will be absolutely out of the question. Two facts are always in favor of the control of this disease: (1) The disease has two hosts and can not pass from pine to pine. (2) The disease is a comparatively slow one; that is, slow as compared with such a disease as the chestnut blight. If at any future time in a completely infected locality the increasing value of the white pine or a change in industrial conditions makes local control profitable such control can be undertaken regardless of the prevalence of the disease at the time, since wherever *Ribes* can be thoroughly eradicated healthy pine stock can be grown and will not take the disease from the already diseased pines.

The entire blister-rust problem is, however, but one phase of a larger problem, which may be stated as follows: does free trade in plant diseases and insect pests pay? Is it an economically sound national policy? Is the entire *importing* nursery business worth as much to the country as the damage which it has already caused? Not a single plant disease or insect pest that has once become established in this country has been eradicated or, in the present state of knowledge, is ever likely to be. No matter how well controlled, it remains in every case a permanent tax against our economic resources. Even if we succeed in controlling the white pine blister rust we may be absolutely certain that other diseases and pests are being introduced which will be just as serious, for we know definitely that the undesirable plant immigrants are not yet all here. It is much more important to safeguard the country against further invasions of this kind than to control this or any other disease or pest that has already been carelessly permitted to establish itself.

It is a matter of common knowledge, which I scarcely need to repeat here, that the countries of Europe, and even ends of the earth like Tasmania and South Africa, have long since protected themselves against the importation of diseases and pests either by prohibition of entry of nursery stock, or by exclusion of large classes of such stock. The United States is far behind in this matter.

The future danger is far greater than the present. The most dangerous class of nursery stock is the ornamental trees and shrubs,

Metcalf: White Pine Blister Rust

Metcalf: White Pine Blister Rust

on account of the great number of species represented, and the widely various parts of the earth from which such stock comes. No section of the country is likely to suffer more from this source than Long Island and the general vicinity of New York City. May I express the hope that this Botanic Garden, already a leader in local and national sentiment in horticultural and botanical affairs, will take a position in this matter which will help to bring about the suppression of this very dangerous traffic?

## EXPLANATION OF PLATES VI AND VII

PLATE VI. A native white pine (*Pinus strobus*) in thick stand, completely girdled by a blister rust canker. Kittery Point, Me. (Photograph by Mr. W. S. Carpenter, of the New York State Conservation Commission.)

PLATE VII. A young native white pine (*Pinus strobus*), completely girdled and showing several infections of blister rust on trunk and branches. Kittery Point, Me. (Photograph by Mr. W. S. Carpenter, of the New York State Conservation Commission.)

# THE ROSY-SPORED AGARICS OF NORTH AMERICA

WILLIAM A. MURRILL

*New York Botanical Garden*

This subtribe of the gill-fungi is characterized by rosy or rosy-ochraceous spores and is well represented by the common and widely distributed species, *Pluteus cervinus*. The North American species may be grouped in ten genera, distinguished by the following key:

## Subtribe PLUTEANAE

| | |
|---|---|
| Pileus irregular, dimidiate or resupinate. | 1. Claudopus. |
| Pileus regular, sometimes eccentric in *Pleuropus*. | |
| Volva and annulus wanting. | |
| Stipe cartilaginous. | |
| Margin of pileus incurved when young. | |
| Lamellae decurrent. | 2. Eccilia. |
| Lamellae adnate or adnexed. | 3. Leptoniella. |
| Margin of pileus straight and appressed when young; lamellae free or adnexed. | 4. Nolanea. |
| Stipe fleshy. | |
| Lamellae decurrent, rarely varying to adnate. | 5. Pleuropus. |
| Lamellae sinuate or adnexed. | |
| Spores not angular, rosy-ochraceous in mass. | 6. Lepista. |
| Spores angular, rose-colored in mass. | 7. Entoloma. |
| Lamellae free. | 8. Pluteus. |
| Volva wanting, annulus present. | 9. Chamaeota. |
| Volva present, annulus wanting. | 10. Volvariopsis. |

A few of these generic names may be unfamiliar to you, such as *Leptoniella* for *Leptonia*, *Pleuropus* for *Clitopilus*, and *Volvariopsis* for *Volvaria*, but these changes have been required by the rules of nomenclature.

The time at my disposal will not permit more than a hasty summary of the North American species belonging to these genera. A fuller treatment may be found in *North American Flora*, volume 10, part 2, to be issued shortly.

### 1. Claudopus

*Claudopus nidulans*, the best known species, occurs throughout Canada and the United States; *C. avellaneus* is known from Oregon only; and there are no species reported from tropical North America.

The other species of the genus occur in the eastern United States, from the Atlantic seaboard to the Rocky Mountains.

### 2. Eccilia

The best known species is *E. atrides*, of the eastern United States. Three species are confined to the Pacific coast, and four to tropical North America.

### 3. Leptoniella

*Leptoniella serrulata*, characterized by the black, serrulate edges of the lamellae, is the best known species. Four are confined to the Pacific coast and seven to tropical North America. The rest occur in the eastern United States.

### 4. Nolanea

The two best known species are *N. conica* and *N. mammosa*, the latter distributed throughout temperate North America but not generally recognized by mycologists. One species is confined to the Pacific coast and three to tropical North America.

### 5. Pleuropus

This genus contains many edible species, among them *P. prunulus*, *P. orcellus*, and *P. abortivus*, the last readily distinguished by the peculiar aborted hymenophores. Two species are confined to the Pacific coast and one to tropical North America.

### 6. Lepista

One of the best edible species we have is *L. personata*, better known as *Tricholoma personatum*. This species and *L. tarda* occur throughout temperate North America. Two other species are confined to the eastern United States, and there are none known from tropical North America.

### 7. Entoloma

This also is a temperate genus, the only species (*E. Murraii*) reaching tropical North America being found in the high mountains of Jamaica. Four species are confined to the Pacific coast. The best known species in the eastern United States are: *E. strictius*, *E. Grayanum*, *E. sericeum*, *E. rhodopolium*, *E. Murraii*, and *E. salmoneum*. Because of the very poisonous European species, *E. lividum*, the members of this genus have been largely avoided by mycophagists.

### 8. Pluteus

The best known species are *P. leoninus* and *P. cervinus*, which are widely distributed. Five species are confined to the Pacific coast and fifteen to tropical North America.

### 9. Chamaeota

Only one species, *C. mammillata*, has been known in this country and this only from Michigan.

### 10. Volvariopsis

The species of this genus are apt to be widely distributed, as is the case with many fungi which inhabit manure. The best known species are probably *V. bombycina*, *V. speciosa*, *V. volvacea*, and *V. pusilla*. Four species are confined to tropical North America.

General Summary

| Genera | Old Species Also in Europe | Old Species America only | New Species | Total |
|---|---|---|---|---|
| *Claudopus* | 4 | 4 | 1 | 9 |
| *Eccilia* | 1 | 15 | 9 | 25 |
| *Leptoniella* | 1 | 28 | 14 | 43 |
| *Nolanea* | 1 | 16 | 11 | 28 |
| *Pleuropus* | 2 | 23 | 5 | 30 |
| *Lepista* | 3 | 1 | 0 | 4 |
| *Entoloma* | 2 | 27 | 34 | 63 |
| *Pluteus* | 2 | 25 | 30 | 57 |
| *Chamaeota* | 0 | 1 | 1 | 2 |
| *Volvariopsis* | 6 | 13 | 2 | 21 |
| 10 | 22 | 153 | 107 | 282 |

# THE CYTOLOGICAL STRUCTURE OF BOTRYORHIZA HIPPOCRATEAE

EDGAR W. OLIVE

*Brooklyn Botanic Garden*

This species of rust, occurring on the host *Hippocratea volubilis* L., was first described by the author, in collaboration with Professor H. H. Whetzel, from material collected in Porto Rico in 1916.[1] It is there recorded as a somewhat peculiar form, though somewhat like a lepto-Uromyces, with only one spore form in its life-cycle. The following diagnosis is there published:[2] "O. Pycnia wanting (probably not formed). III. Telia mostly hypophyllous but sometimes amphigenous or caulicolous, generally from a localized mycelium, sometimes from a systemic invasion affecting entire young shoots; localized sori densely crowded in more or less orbicular or irregularly shaped, somewhat hypertrophied pulvinate areas, 1 mm.–1 cm. or more across, the affected areas yellowish when young, when older becoming whitish due to the germination of the spores; in older leaves often killing affected spots, which turn brown, the resultant rounded, swollen dead areas then bearing a striking resemblance to certain insect galls.

"Telia pulverulent, erumpent, from a definite, superficial, uredinoid hymenium which arises just under the epidermis, without peridium; teliospores uninucleate, borne singly at the end of pedicels which arise from a binucleate mycelium 13–14 by 18–24 $\mu$, thin-walled, óval, with a rounded apical protuberance, germinating apically at maturity to produce each a long, cross-septate basidium (promycelium) bearing 4 basidiospores (sporidia), similar in shape to the teliospores and 8 by 11–12 $\mu$.

"Vegetative mycelium composed of coarse intercellular hyphae, made up of binucleated cells, some of which send large botryose, or irregularly shaped, haustoria into adjacent cells."

The generic name, *Botryorhiza*, is, in fact, derived from the botryose character of the haustoria, a striking feature which, so far as I am aware, is possessed rarely if at all by other rusts. It is, however,

[1] Endophyllum-like rusts of Porto Rico. Amer. Journ. Botany. 4: 44–52. *pls. 1–3.* 1917.

[2] L. c., p. 47.

pointed out in the above mentioned paper, that certain smuts (as *Doassantia deformans*, *e. g.*) also possess botryose haustoria.[3]

The 18 figures in Plate VIII show fairly clearly the salient features of the cytological structure and development of *Botryorhiza*, with the exception of the sexual fusions, which have not as yet been found. Undoubtedly, however, these fusions and the consequent transition from the uninucleate condition initiated in the germinating promycelium to the binucleate condition prevalent in the vegetative mycelium, must take place early in the development of the latter.

Two hypophyllous sori are shown in Fig. 1, the one at the right a very young one pushing through a stoma. The mycelium and hymenial hyphae are seen to be composed of binucleate cells, as is also the case of the young spores. Two of the peculiar botryose haustoria are shown at the lower portion of the figure, nearly filling the host cells. Fig. 2 shows a portion of the coarse, branched, intercellular mycelium, with some its binucleate cells. This mycelium varies from about 5 to 7 $\mu$ in diameter. One cell is shown with four nuclei, evidently a result of a recent conjugate division. The conspicuous thickenings drawn along the edges of the hypha are colored red in the preparation with Flemming's triple stain; their mode of origin and significance still remain to be solved.

Figs. 3–7 show five varying views of the large botryose haustoria. The narrow isthmus connecting the enlarged haustorium with the extra-cellular mycelium is clearly shown in each case, as is also the interesting fact that the haustorium, even in those cases in which the host cell is almost entirely filled by it, pushes in as it grows the plasma membrane of the host protoplasm. Strictly speaking, therefore, in no case is the haustorium really *inside* the host protoplasm. Fig. 3 is a section of a young haustorium showing this invagination of the host cytoplasm. Four nuclei of the rust are also shown in this preparation. In Fig. 4 an older haustorium showing its peculiar botryose swellings, has pushed up into an unusually dense mass of host cytoplasm, now shrunken away from the invaginated haustorium. Figs. 5, 6, and 7 show almost equally clearly this phenomenon of invagination of the host cytoplasm. In Fig. 5, particularly, the haustorium is seen to almost fill the host cell. An idea of the large size of the haustoria may be gained from the fact that while the cells of the leaf of the host *Hippocratea* measure from 15 to 20 $\mu$ in diameter, those of the fungous haustoria range from about 10 to 14 $\mu$ in diameter.

Figs. 8 to 14 show various stages in the formation and germination of the teliospores. Fig. 8 is of a young sporiferous hypha showing two

[3] Lutman, B. F. Some contributions to the life history and cytology of the smuts. Trans. Wis. Acad. Sci. 16: 1191–1244. 1910. See his Figs. 44 and 45.

pairs of conjugate nuclei, those of the stalk and also those of the young spore, which is shown in process of abstriction. As in other cases of cell-division among fungi and algae, a ring-formed constriction grows in from the periphery, thus cutting off in this instance the binucleate spore from the binucleate stalk cell. Fig. 9 is a drawing of such a young spore, showing the two nuclei; in Fig. 10, the two nuclei have fused, though it is evident from the presence of the two nucleoles that this fusion has only recently taken place. Figs. 11 and 12 represent mature spores, each borne on binucleate stalks, the latter figure showing the apical protuberance so characteristic of most spores. That this protuberance is the primordium of the apical germ-tube is apparent from a perusal of Figs. 13 and 14. These spores, as is stated above, germinate at once on maturity. In Fig. 14, the heterotypic nuclear division is proceeding; this, however, is so poorly stained in the preparation, that it is not possible to make out the details of the process. Figs. 15, 16, and 17 show the basidia, or promycelia, each composed of four uninucleate cells, which result from the germination of the teliospores. In Fig. 15 appears a type of germination which apparently results from growth of the basidium in a very damp situation; the four cells of the basidia in such cases often break apart and function independently. Fig. 16 shows the more usual type of germination, in which each of the four cells sends out a branch, to bear finally at the tip of each a single uninucleate basidiospore on a sterigma. Two of these oval basidiospores are shown in Fig. 18.

## General Discussion

It will be seen from these figures and the accompanying description that while *Botryorhiza* undoubtedly resembles a short-cycled lepto-Uromyces in the one-celled character of its teliospores, it is sufficiently distinct in other respects to justify its being placed in a new genus. Some of these differences are as follows: the walls of the teliospores in *Botryorhiza* are thin instead of thickened, as is usual in *Uromyces;* they are colorless, instead of brown or otherwise colored, as in *Uromyces;* there are no germ-pores in the walls of the spores of *Botryorhiza*, whereas the teliospores of *Uromyces* are characterized by one or more. Finally, the possession of such strikingly large, botryose haustoria, so characteristic of *Botryorhiza*, is, in my opinion, a very distinctive feature.

Apparently the more usual type of rust haustorium, so far as our few studies on the subject have revealed, is that of an irregular, branching hypha. Atkinson[4] has, however, figured the haustoria of *Uromyces caryphyllinus* as somewhat irregular and botryose in form;

[4] College Botany. Henry Holt & Co. P. 87.

and Pole Evans[5] in his careful investigation of the histology of nine species of cereal rusts has shown that while the young haustoria of various species may be small and sac-like, or even "hammer-headed" in others, the prevailing type of mature haustoria in these cereal rusts seems to be the cylindrical or branched form.

Attention was called in the earlier description of *Botryorhiza* to the fact that Lutman had figured botryose haustoria in *Doassantia* and it was there suggested that this Porto Rican rust might have some other features in common with smuts. But the fact that the sporiferous hyphae are sent out through a stoma or through the ruptured epidermis before the spores themselves are cut off from their tips, and, further, that there is produced in *Botryorhiza* (and apparently in rusts in general) a definite, *superficial hymenial layer* from which the spores arise constitutes two essential points of difference from the smuts. The latter, as Lutman has clearly emphasized,[6] have their spores produced either from a group of deeply imbedded multinucleate hyphae, which break up directly into spores (in the Ustilaginaceae) or from the tips of the side or main branches of the prevailingly binucleate hyphae (as in the Tilletiaceae).

It has also been brought out in the description of the characteristics of *Botryorhiza* that the mycelium is composed of a branching system of very coarse hyphal threads. These hyphae measure from 5 to 7 $\mu$ in diameter. In my own work on various rusts, I had never before met with such a coarse mycelium. Pole Evans,[7] however, has called attention to the fact that the mycelial threads of *Puccinia glumarum* reach the relatively enormous size of 10 to 19 $\mu$ in diameter; also Dodge in his paper in this Memoir[8] has noted that Farlow[9] and Wörnle[10] have found the hyphae in *Gymnosporangium Ellisii* to be exceptionally large, being, according to the latter author, about 8 $\mu$ in diameter.

[5] The cereal rusts. I. The development of their uredo mycelia. Annals of Botany **21**: 441–446. 1907.

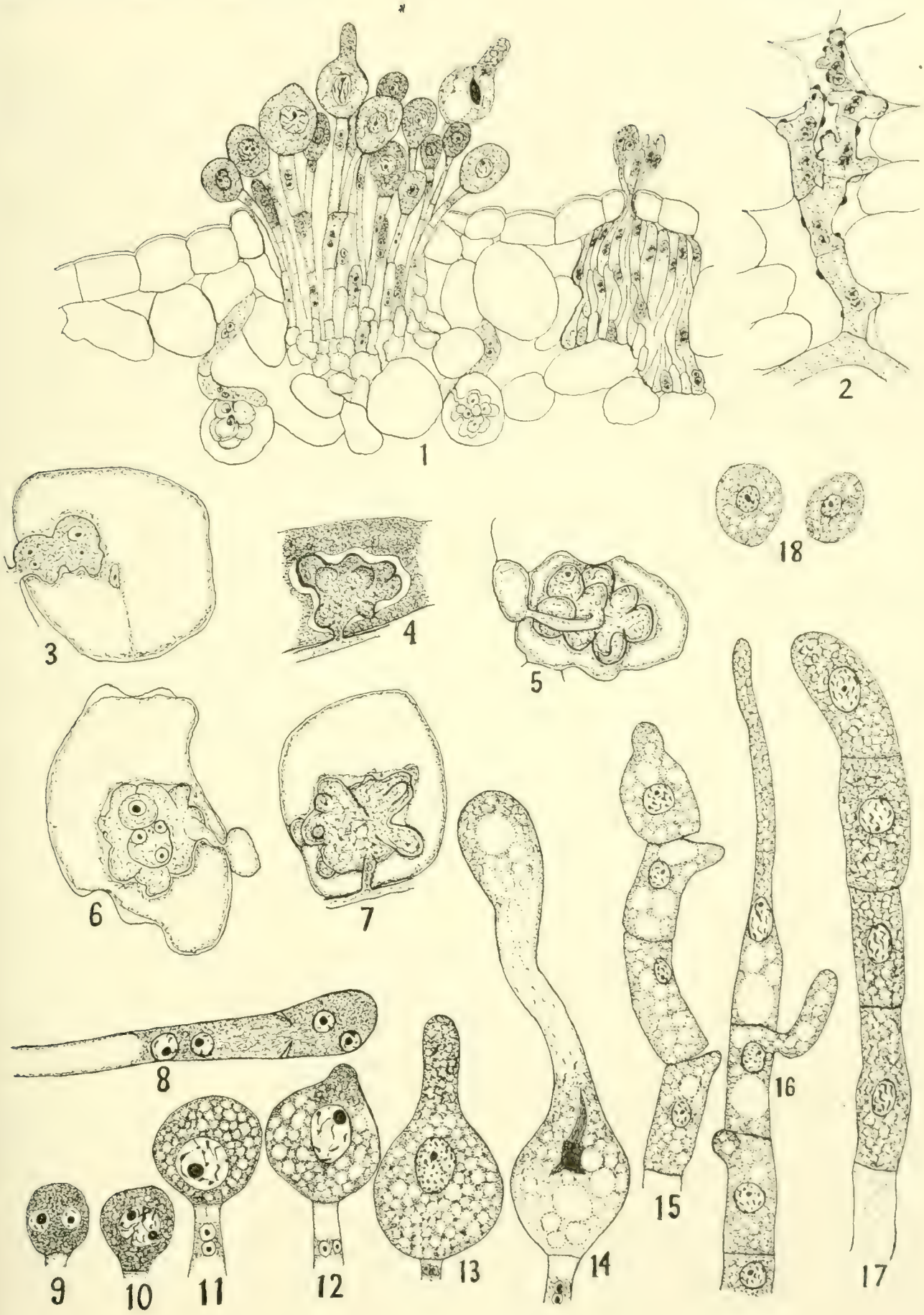
[6] L. c., p. 1218.

[7] L. c., p. 451.

[8] See p. 128.

[9] The gymnosporangia of the United States. Ann. Mem. Boston Soc. Nat. Hist. 1880: 1–38.

[10] Anatomische Untersuchung der durch Gymnosporangium-Arten hervorgerufenen Missbildungen. Forst. Nat. Zeits. **3**: 68–84; 129–172. 1894.




OLIVE: CYTOLOGICAL STRUCTURE OF BOTRYORHIZA

## EXPLANATION OF PLATE VIII

All drawings have been made with the camera lucida, and with various combinations of Zeiss apochromatic lenses. Except where otherwise noted, the magnification has been 1,000 diameters.

*Botryorhiza Hippocrateae* Whetzel & Olive

FIG. 1. Two young sori, showing the hymenial layer, composed of binucleate cells, and method of spore formation. At the right a young sorus pushing through a stoma. Somewhat diagrammatic. × 500.

FIG. 2. Branching hypha, showing the binucleate cells, whose walls in some places show peculiar thickenings. × 500.

FIG. 3. Young haustorium, containing 4 nuclei. Note the invagination of the host cytoplasm.

FIG. 4. Another haustorium, pushing into a mass of dense, granular host protoplasm.

FIG. 5. A fully mature haustorium, showing its botryose lobings.

FIGS. 6 and 7. Haustoria in partial section; showing the pushing in of host protoplasm.

FIG. 8. A young hypha from the hymenium, showing the constricting wall cutting off stalk from spore. × 1,500.

FIG. 9. A young spore, with two nuclei.

FIG. 10. A young spore in which the two nuclei have just fused, as evidenced by the presence of two nucleoles.

FIGS. 11 and 12. Mature teliospores, showing binucleate stalks.

FIG. 13. A spore showing young germ-tube.

FIG. 14. Another spore, with growing basidium, or promycelium. The nucleus is in metaphase of the heterotypic division; but the preparation is poorly stained.

FIGS. 15, 16 and 17. Three basidia, which have divided into the characteristic 4 cells. Fig. 16 shows the branches, each of which will bear ultimately a single basidiospore.

FIG. 18. Two basidiospores, showing the uninucleate condition.

# THE NUCLEUS AS A CENTER OF OXIDATION

W. J. V. OSTERHOUT

*Harvard University*

In 1897 Spitzer[1] reported that nucleoproteins extracted from certain animal tissues possess the same oxidizing power as the tissues themselves. The idea that the nucleus is a center of oxidation was advocated by Loeb[2] who pointed out that it would explain why cells deprived of their nuclei are unable to live for a long time or to regenerate missing parts.

R. Lillie[3] sought to obtain direct experimental evidence by applying to the cell reagents which become colored on oxidation. The reagent chiefly employed was a mixture of alpha naphthol and paraphenylene diamine which yields upon oxidation a deep purple dye, indophenol. The oxidation takes place slowly on exposure to air, but is greatly accelerated in the presences of living cells or extracts of living tissues. Lillie found that in certain tissues of the frog (especially liver, kidney and leucocytes) the colored oxidation products were deposited in and about the nucleus, especially at the surface of contact between nucleus and cytoplasm.

Wherry[4] applied methyl green to *Amoeba* and reported that it was oxidized in the cytoplasm but not in the nucleus. Schultze[5] applied a number of stains to plant and animal cells and found that they were oxidized in the cytoplasm but not in the nucleus.

Unna[6] has investigated a large number of cases by the use of leucomethylene blue and has reached the conclusion that the nucleus is a center of oxidation. Unna's theories have been criticized by Oppenheimer[7] and by Schneider.[8]

Mathews[9] has come to the conclusion that the nucleus is directly concerned in oxidation.

[1] Pflüger's Archiv. **67**: 615. 1897.

[2] Archiv. f. Entwickelungsmechanik der Organismen **8**: 689. 1899.

[3] American Jour. of Physiology **7**: 412. 1902.

[4] Wherry, E. T. Science, N. S. **37**: 908. 1913.

[5] Schultze, W. H. Verhandl. d. deutsch. path. Ges. **16**: 161. 1913.

[6] Unna, P. G. Archiv. f. mikr. Anat. 78. 1911. Godoletz, P. und Unna. P. jun. Berlin, klin. Wochenschrift **49**: 1134. 1912. Unna, P. G. und Godoletz, L. Oppenheimer's Handb. d. Biochem. Erganzungsband. 1913. S. 327.

[7] Oppenheimer, C. Die Fermente und ihre Wirkung **2**: 790, 810. 1913.

[8] Schneider, H. Zeit. wiss. Mikr. **31**: 478. 1914.

[9] Mathews, A. P. Physiological Chemistry p. 180. 1915.

Warburg[10] found that it was possible to isolate the nuclei from erythrocytes of birds (by freezing and thawing) and that such nuclei consumed oxygen about as rapidly as the normal cells. While this indicates that the nucleus is the principal agent in oxidation other experiments of Warburg have been interpreted to indicate that oxidation is practically confined to the surface of the cell.[11] In these experiments[12] it was found that NaOH greatly increased oxidation in the sea-urchin egg but did not penetrate sufficiently to cause a change of color in eggs stained with neutral red. In a later paper R. Lillie[13] comes to the conclusion that rapid oxidation occurs at the surface of the cell as well as at the surface of the nucleus. This conclusion is based upon a study of the indophenol reaction in the corpuscles of frog's blood.

The use of the indophenol reaction may encounter an objection on the ground that the result may depend to a considerable extent on the manner in which the reagent penetrates. If the oxidizing substances of the cell are largely concentrated in the nucleus those which are present in the cytoplasm will first meet the reagent at the cell surface and may produce at that point a deposit of granules of indophenol. In the same manner the oxidizing substances which are retained within the nucleus will first meet the reagent at the surface of the nucleus and produce a deposit in that region.

If, therefore, the indophenol reaction shows a higher oxidative activity in the nucleus it may doubtless be depended on, since its error presumably lies in the opposite direction. But if it indicates a marked oxidative activity at the surface of the cell (or at internal surfaces, including that of the nucleus) we must be cautious in drawing conclusions.

It would seem that more reliable evidence can be obtained by investigating cases where it is not necessary that the reagent should penetrate from without owing to the fact that the cell itself produces substances which become colored on oxidation.

The writer has investigated a case of this kind. The plant chosen was the Indian Pipe, *Monotropa uniflora*, which is extremely well suited to such investigations because the colorless cells contain a chromogen which oxidizes and darkens very rapidly upon injury. An addi-

[10] Warburg, O. Zeit. f. physiol. chem. **70**: 413. 1910–11.

[11] This interpretation is by no means necessary. Cf. Loeb and Wasteneys, Jour. of Biochemistry **14**: 459. 1913; **21**: 153. 1915; also, Osterhout, ibid. **19**: 335. 1914. Owing to the buffer action of protoplasm and to the presence of pigment the penetration of a small amount of alkali is not easily detected.

[12] Warburg, O. Zeit. f. physiol. chem. **66**: 305. 1910. Biochem. Zeit. **29**: 414. 1910.

[13] Jour. of Biol. Chem. **15**: 237. 1913.

tional advantage is that the leaves are so thin and transparent that they may be placed under the microscope and the details of cell structure studied with care before the cells are injured or treated with reagents.

In a typical leaf cell the cytoplasm is transparent and nearly colorless, with a few granules, while the nucleus is only slightly less transparent and as a rule shows a few granules and a nucleolus. When a leaf is mounted in a drop of water under a cover glass the cells remain unchanged in appearance for hours.

If an intact portion of the leaf is cut or crushed the cells in the neighborhood of the injury soon change their appearance. In the course of five or ten minutes the nuclei of the cells nearest the injury assume a more granular (or vacuolated) appearance and soon begin to darken. The darkening does not begin at the surface but appears to take place almost simultaneously throughout the whole mass of the nucleus. Not until the nucleus has become very dark (so as to stand out very conspicuously when the preparation is viewed under the low power of the microscope) does the cytoplasm begin to darken perceptibly. It may be several hours after the nucleus has darkened before a change of color can be perceived in the cytoplasm. (This is also true where the thickness of the cytoplasm has been increased by plasmolysis so as to be as great as that of the nucleus.) The darkening of the cytoplasm does not seem to be more rapid at the surface than elsewhere.

That the darkening is due to oxidation is shown by several facts. Among these the following may be mentioned.

1. A microscope slide is smeared with vaseline, a leaf is laid upon the vaseline and more vaseline is carefully placed upon the leaf. A small splinter of glass (from a broken slide) is placed on the leaf and another slide is gently pressed upon it, so as to spread the vaseline and bring the glass splinter close to the leaf without injuring the latter. Care should be taken that any air bubbles which may be included in the vaseline are not in contact with the leaf in the neighborhood of the splinter of glass.

The leaf is left over night in order that the oxygen present in the intercellular spaces (or adhering to the surface of the leaf) may be used up by respiration. On the following morning the upper slide is pressed down with sufficient force to drive the splinter into the leaf and crush it. It is then placed on the stage of the microscope and kept under observation. It is found that while some darkening occurs it is at first largely confined to the drops of juice forced out of the leaf by the crushing (the juice seems to spread along the fibro-vascular bundles in some cases). The darkening of the nucleus and cytoplasm is usually much slower than in air (especially with fresh leaves).

The darkening which occurs is due in part to free oxygen left in the leaf and in part to oxygen in compounds from which it can be split off for the oxidation of the chromogen (analogous to anaërobic respiration).

2. If leaves are torn in two or crushed at once, dropped into boiling water, 0.1 *M* HCl, 0.1 *M* NaOH, 0.1 *M* KCN, or 3 percent $H_2O_2$ the darkening does not occur. These agents are inhibitors of oxidation in living tissues. Hydrogen peroxide may inhibit at high concentration, but accelerate at low concentrations. In NaOH and KCN the leaf becomes pale yellow: this seems to be due to the action of hydroxyl ions.

3. The chromogen may be extracted by placing stems in 0.1 *M* NaOH in a bottle completely filled (so as to exclude air) and tightly stoppered (with a glass stopper coated with vaseline). The solution becomes pale yellow (or slightly reddish) and may be kept in this condition for months. On opening the bottle and pouring out the solution into a shallow dish it at once becomes red as the result of oxidation. The behavior seems to be analogous to that of pyrogallol, which is easily oxidized by the air in alkaline solution, but not in neutral solution except under the influence of oxidases (from plants or animals) or other catalyzers.

That the darkening of the nucleus is due to oxidation taking place in the nucleus itself and not to the taking up by the nucleus of a stain produced in the cytoplasm or vacuoles is shown by the following experiment. Plants were ground in a mortar and allowed to stand until they became black. The juice was squeezed out and centrifuged, giving an inky fluid. In this were placed pieces of leaves which had been treated with 0.1 KCN and afterward with water. The solution was allowed to stand until it became concentrated by evaporation: it then appeared black. It was found that where the nuclei had been squeezed out of the cut cells by the knife they had taken up some stain but not more than the cytoplasm. In cells which were merely cut open there was little or no staining of the nucleus.

We must therefore conclude that oxidation occurs more rapidly in the nucleus than elsewhere in the cell. The only way to escape this conclusion would be by assuming that at the moment of injury there is a sudden migration into the nucleus of some or all of the substances necessary for the oxidation. This is not only very improbable from a theoretical standpoint, but observation shows that it can not be the case, for in this migration the substances would mingle and produce the pigment either outside the nucleus or at its surface before any pigment appeared in the interior of the nucleus. Observation of the nucleus shows that the pigment appears as soon in the interior of the nucleus as at its surface.

We may therefore conclude that the substances necessary for oxidation do not suddenly migrate into the nucleus at the moment of injury, but that they must exist there before the cell is injured.

We may ask why the nucleus does not become darkened in the normal condition of the cell. The investigations of several workers have made it probable that the pigments produced by oxidation under normal conditions are at once reduced, giving up their oxygen to other substances in the cell. When injury occurs the reduction is checked more rapidly than the oxidation, with the result that the pigment accumulates.

It is also possible that injury causes the admission of oxygen to the cells.

In order to test the effect of the indophenol reaction on leaves of *Monotropa* they were torn in two and placed in a mixture of equal parts of aqueous 1 percent paraphenylene diamine and saturated aqueous alpha naphthol. It was found that the result depends somewhat on the condition of the reagent. In the most favorable cases the cells which were torn open became pale purple in color almost at once, showing that the reagent readily penetrated them. Usually the cell contents (cytoplasm, nucleus and vacuole) became at first uniformly tinged with purple. After a while the nuclei would usually assume a deeper purple than the remainder of the cell contents.

The cells lying a little further from the torn surface, which were injured but not actually torn open, showed at first a pale yellowish color which in some cases became deeper with time and in other cases gave way to a purplish tint. In most of these cells the nuclei gradually became deeper in color than the other cell contents. Later the cytoplasm became in some cases so deep in color as to obscure the nuclei. Cells lying still further from the torn surface changed very slowly (many remaining unchanged after some hours) so that it was evident that the reagent penetrated from the torn surface and not through the outer cell walls (which are normally in contact with the air.[14]

In most cases the general result, after a few minutes, was a deep purple band along the torn edge: inside the purple band was a yellowish one of irregular outline, followed by nearly colorless intact cells further away from the torn edge.

In 1 percent aqueous paraphenylene diamine the results were similar but the purple color was replaced by a dirty brownish-red (with more or less purplish tinge).

It should be pointed out that these results are most striking with

[14] More rapid penetration from cut or torn surfaces is commonly observed in the entrance of reagents into leaves, petals, etc.

reagents which have stood long enough to take up oxygen, in consequence of which the paraphenylene diamine becomes reddish in color, while the alpha naphthol assumes a dirty grayish-purple.

When the reagents are freshly made up the action is very slow unless hydrogen peroxide be added. When a mixture is made up of equal parts of each of the reagents previously mentioned and 0.3 percent hydrogen peroxide the results are similar to those just described. But if stronger hydrogen peroxide be used a greater amount of purple coloration is observed in the cells.

When 3 percent hydrogen peroxide is used (in place of 0.3 percent) the following changes may be observed. A pronounced purple color appears at once in the torn cells: this spreads rapidly to the adjacent cells, which are still intact, and may extend through several rows of intact cells. In these intact cells the first appearance of change is the formation of purple granules of indophenol in the vacuole. The vacuole becomes filled with these granules which show active Brownian movement. Occasionally some of them come in contact with the nucleus (or the film of cytoplasm which covers the nucleus) and stick fast to it. At this time nucleus and cytoplasm are usually free from granules or coloration. The purple color grows more intense until the details of cell structure become obscured.

The general conclusion is that while the indophenol reaction indicates that the nucleus is the center of oxidation it does not give as definite information on this point as the formation of natural pigments within the cell as the result of the oxidation of substances normally present.

## Summary

Injury produces in the leaf-cells of the Indian Pipe (*Monotropa uniflora*), a darkening which is due to oxidation. The oxidation is much more rapid in the nucleus than in the cytoplasm and the facts indicate that this is also the case with the oxidation of the uninjured cell.

# PHYSIOLOGICAL SPECIALIZATION OF PARASITIC FUNGI

GEORGE M. REED

*University of Missouri*

One of the important developments in plant pathology in recent years has been the discovery of races of well-defined morphological species of parasitic fungi which are restricted to particular hosts. These specialized races can be distinguished from each other only by their ability to grow on some host plants and not on others. It is now well established that species of parasitic fungi, identical in their structural features as found on a more or less wide range of plants, may consist of numerous races or strains which differ in their capacity to infect the various hosts.

Apparently Schroeter (136), as early as 1879, was the first to call attention to this phenomenon in connection with certain rusts on *Carex*. It is, however, to Eriksson (34) that we are indebted for a realization of the importance and significance of the host specialization of fungous parasites and for the impetus to the numerous investigations devoted to this phase of plant pathology. Eriksson's demonstration of races of *Puccinia graminis*, *P. glumarum*, *P. dispersa* and *P. coronata*, distinguishable from each other only on the basis of the hosts that they are able to successfully attack, is the real starting point for a general recognition of the phenomenon of host specialization of fungous parasites.

Various terms have been introduced to apply to these races or strains which show no anatomical differences, but are distinguishable only by their physiological behavior in the choice of hosts. Schroeter (138), in 1893, suggested the term *sister species* (*Species sorores*). Klebahn (76), in 1892, described them as *biologische Spezies*. Rostrup (121, 122), in 1894, suggested the term *biologiske Arter*, and, in 1896, proposed another term *biologische Rassen*. In 1894 Hitchcock and Carleton (63) proposed the term *physiological species*. Eriksson (34), in 1894, introduced the generally used expression *Specialisierte Formen* or *formae speciales*. Magnus (96), in 1894, employed the term *Gewohnheitsrassen* or *adapted races*. Marchal (97) applied the term *races spéciali ées*, while Ward (174), Salmon (123) and others have used the expression *biologic forms* or *biological forms*.

Whatever term has been applied, the underlying conception has been the same, namely, that these races, strains, forms, etc., of distinct morphological species of fungous parasites differ, not in discernible structural features, but in their physiological behavior, as indicated by their ability to infect some hosts and not others. They differ in their ability to establish the parasitic relation with particular hosts and thus secure the necessary food for their normal development. The phenomenon is distinctly physiological and is doubtless quite comparable to the well-known behavior of saprophytic fungi on different chemical substrata. Various saprophytes, structually similar, vary in their ability to utilize different chemicals as sources of food, dependent on their capacity to secrete the necessary enzymes. While the strains of parasites may differ essentially in their ability to secure food from a particular host, we must keep in mind the possibility of a more complicated series of relations in which toxin and antitoxin production are involved.

Many investigators of the phenomenon of host specialization have made a large number of species on the basis of the results of their inoculation tests. This is especially the case in the rusts where Klebahn, Eriksson, Schneider, Fischer and others have raised many forms to specific rank, although no distinct structural differences can be observed. It may be noted that the races of *Puccinia dispersa*, *P. sessilis*, *P. Ribesii-Caricis*, *P. extensicola*, *Coleosporium Campanulae*, *Melampsora populina*, *M. Tremulae* and others, referred to below, are regarded as good species by some students.

Fischer (45), in connection with the rusts, accepts as species the following:

1. All rusts which are structurally distinct.
2. All rusts which have a different life-cycle; for example, forms which are distinguished by the presence or absence of certain spore-forms.
3. All forms which differ in their choice of hosts, in so far as the hosts belong to different genera. In heteroecious rusts species are recognized when the hosts of one generation, aecidial or uredo and teleuto, belong to two different genera.

Fischer unites under one species as *formae speciales* or specialized races all rusts which differ only physiologically and whose hosts are species of a single genus. Whether a particular rust is a *physiological species* or a *specialized race* is thus determined by the range of its hosts.

It is doubtless true that many rusts, and other parasitic fungi as well, which can be distinguished only by the hosts upon which they grow, are just as distinct forms as others which are characterized by

minute structural differences. The poplar rusts of the group *Melampsora Tremulae*, with their uredo and teleuto stages on *Populus alba* and *P. tremula* and their aecidial stage on such widely separated hosts as *Larix decidua*, *Pinus silvestris*, *Mercurialis perennis* and *Chelidonium major*, certainly differ from each other in a fundamental way. The difference between these is doubtless as significant as some of the minute structural differences which distinguish other species.

It is, however, certainly important to recognize the fact that these rusts, mildews, etc., referred to as specialized races, physiological species, etc., can be distinguished only by cultural tests. This can most easily be done by grouping them together on the basis of structural similarity. Klebahn (92) has done this recently in his scheme for illustrating the relationships of the willow and poplar rusts, and also in the case of the *Ribes-Carex* rusts. Arthur (10) adopts the same plan in combining the *Compositae-Carex* rusts under *Puccinia extensicola* Plowr. In a similar way Tranzschel (155) combines the various *Centaurea-Carex* rusts under the name *Puccinia Centaureae-Caricis*.

At the present time, a large number of the parasitic fungi have been investigated from the standpoint of specialization to particular hosts and the phenomenon has been found to be of wide occurrence. The present paper is an attempt to bring together the results of numerous investigations bearing on this point.

## The Rusts—Uredineae

**Puccinia graminis** Pers. Extensive studies have been made in both Europe and the United States on the specialization of the black stem rust of the cereals and other grasses. Eriksson (34, 37, 38, 41) in Sweden, Jaczewski (68) in Russia, Carleton (25, 26), Freeman and Johnson (57), Arthur (2, 5, 6, 7, 8, 10, 11), and Stakman and coworkers (143–149) in the United States, have reported the results of their cultural experiments with this rust. Experiments have been reported in which inoculation tests with both uredospores from the various grass hosts and aecidiospores from the barberry have been used. The general results of these experiments may best be summarized as follows:

SPECIALIZED RACE *Avenae*

| Sweden—Eriksson | Russia—Jaczewski | United States—Carleton | United States—Stakman and Piemeisel |
|---|---|---|---|
| *Avena sativa.* | *Avena sativa.* | *Avena sativa.* | *Avena sativa.*[1] |
| *Avena brevis.* | *Avena pubescens.* | *Avena fatua.* | *Avena fatua.*[1] |
| *Avena sterilis.* | *Alopecurus pratensis.* | *Avena hookeri.* | *Agropyron cristatum.*[3] |
| *Alopecurus pratensis.* | *Arrhenatherum elatius.* | *Avena pratensis.* | *Agrostis alba.*[3] |
| *Arrhenatherum elatius.* | *Briza media.* | *Avena sterilis.* | *Agrostis exarata.*[1] |
| *Briza maxima.* | *Bromus arvensis.* | *Agrostis scabra.* | *Agrostis stolonifera.*[3] |
| *Bromus arvensis.* | *Festuca ovina.* | *Alopecurus alpestris.* | *Alopecurus geniculatus.*[2] |
| *Bromus brachystachys.* | | *Ammophila arenaria.* | *Alopecurus pratensis.*[2] |
| *Bromus madritensis.* | | *Arrhenatherum elatius.* | *Anthoxanthum puelli.*[1] |
| *Dactylis glomerata.* | | *Bromus ciliatus.* | *Arrhenatherum elatius.*[2] |
| *Festuca myurus.* | | *Dactylis glomerata.* | *Beckmannia eruciformis.*[3] |
| *Festuca sciuroides.* | | *Eatonia obtusata.* | *Bromus erectus.*[3] |
| *Festuca tenuiflora.* | | *Festuca sp. indet.* | *Bromus purgans.*[3] |
| *Koeleria setacea.* | | *Holcus mollis.* | *Bromus tectorum.*[2] |
| *Lamarckia aurea.* | | *Hordeum murinum.* | *Calamagrostis canadensis.*[2] |
| *Milium effusum.* | | *Koeleria cristata.* | *Dactylis glomerata.*[1] |
| *Phalaris canariensis.* | | *Phleum asperum.* | *Elymus canadensis.*[3] |
| *Phleum asperum.* | | *Polypogon monspeliensis.* | *Elymus robustus.*[3] |
| *Trisetum distichophyllum.* | | *Trisetum subspicatum.* | *Festuca elatior.*[3] |
| *Vulpia bromoides.* | | | *Festuca ovina.*[3] |
| | | | *Holcus lanatus.*[2] |
| | | | *Hordeum pusillum.*[3] |
| | | | *Hordeum spontaneum.*[3] |
| | | | *Hordeum vulgare.*[3] |
| | | | *Hordeum vulgare pallidum.*[3] |
| | | | *Hordeum vulgare pallidum pyramidatum.*[3] |

[1] Hosts on which the race was found in nature.

[2] Hosts heavily infected by artificial inoculation.

[3] Hosts slightly infected by artificial inoculation.

| Sweden—Eriksson | Russia—Jaczewski | United States—Carleton | United States—Stakman and Piemeisel |
|---|---|---|---|
| | | | SPECIALIZED RACE *Avenae—Continued* |
| | | | *Hystrix patula.*[3] |
| | | | *Koeleria cristata.*[1] |
| | | | *Lolium italicum.*[3] |
| | | | *Lolium perenne.*[3] |
| | | | *Lolium temulentum.*[3] |
| | | | *Panicularia pauciflora.*[1] |
| | | | *Phalaris canariensis.*[2] |
| | | | *Phleum pratense.*[3] |
| | | | *Secale cereale.*[3] |
| | | | SPECIALIZED RACE *Secalis* |
| *Secale cereale.* | *Secale cereale.* | | *Secale cereale.*[1] |
| *Agropyron caninum.* | *Agropyron caninum.* | | *Agropyron caninum.*[1] |
| *Agropyron desertorum.* | *Agropyron repens.* | | *Agropyron cristatum.*[1] |
| *Agropyron repens.* | *Bromus inermis.* | | *Agropyron elongatum.*[2] |
| *Bromus secalinus.* | *Bromus secalinus.* | | *Agropyron imbricatum.*[3] |
| *Elymus arenarius.* | *Dactylis glomerata.* | | *Agropyron intermedium.*[3] |
| *Elymus sibiricus.* | | | *Agropyron repens.*[1] |
| *Hordeum comosum.* | | | *Agropyron sibericum.*[3] |
| *Hordeum jubatum.* | | | *Agropyron smithii.*[1] |
| *Hordeum murinum.* | | | *Agropyron tenerum.*[1] |
| *Hordeum vulgare.* | | | *Avena sativa.*[3] |
| | | | *Bromus purgans.*[3] |
| | | | *Bromus tectorum.*[2] |
| | | | *Elymus canadensis.*[1] |
| | | | *Elymus robustus.*[1] |
| | | | *Elymus virginicus.*[2] |
| | | | *Hordeum jubatum* [1] |
| | | | *Hordeum pusillum.*[1] |

SPECIALIZED RACE *Secalis—Continued*

| Sweden—Eriksson | Russia—Jaczewski | United States—Carleton | United States—Stakman and Piemeisel |
|---|---|---|---|
| | | | *Hordeum spontaneum.*[2] |
| | | | *Hordeum vulgare.*[1] |
| | | | *Hordeum vulgare pallidum.*[2] |
| | | | *Hordeum vulgare pallidum pyramidatum*[2] |
| | | | *Hystrix patula.*[1] |
| | | | *Sporobolus cryptandrus.*[1] |
| | | | *Triticum vulgare.*[3] |

SPECIALIZED RACE *Tritici*

| | | | |
|---|---|---|---|
| *Triticum vulgare.* | *Triticum vulgare.* | *Triticum compactum.* | *Triticum compactum.*[1] |
| *Avena sativa.* | *Agropyron repens.* | *Triticum durum.* | *Triticum dicoccum.*[1] |
| *Hordeum vulgare.* | *Agropyron caninum.* | *Triticum monococcum.* | *Triticum durum.*[1] |
| *Secale cereale.* | *Festuca gigantea.* | *Triticum polonicum.* | *Triticum monococcum.*[1] |
| | *Hordeum vulgare.* | *Triticum turgidum.* | *Triticum polonicum.*[1] |
| | *Lolium perenne.* | *Triticum villosum.* | *Triticum Spelta.*[1] |
| | | *Triticum vulgare.* | *Triticum turgidum.*[1] |
| | | *Agropyron richardsoni.* | *Triticum vulgare.*[1] |
| | | *Agropyron tenerum.* | *Agropyron caninum.*[1] |
| | | *Dactylis glomerata.* | *Agropyron cristatum.*[1] |
| | | *Elymus canadensis.* | *Agropyron elongatum.*[3] |
| | | *Elymus virginicus.* | *Agropyron intermedium.*[3] |
| | | *Festuca gigantea.* | *Agropyron repens.*[3] |
| | | *Hordeum jubatum.* | *Agropyron smithii.*[1] |
| | | *Hordeum murinum.* | *Agropyron spicatum.*[1] |
| | | *Hordeum vulgare.* | *Agropyron tenerum.*[1] |
| | | *Koeleria cristata.* | *Alopecurus pratensis.*[3] |
| | | | *Avena sativa.*[3] |
| | | | *Bromus hordeaceus.*[2] |
| | | | *Bromus pumila.*[2] |

SPECIALIZED RACE *Tritici—Continued*

| Sweden—Ericksson | Russia—Jaczewski | United States—Carleton | United States—Stakman and Piemeisel |
|---|---|---|---|
| | | | *Bromus tectorum.*[2] |
| | | | *Elymus brachystachys.*[1] |
| | | | *Elymus canadensis.*[1] |
| | | | *Elymus macounii.*[1] |
| | | | *Elymus robustus.*[1] |
| | | | *Elymus virginicus.*[1] |
| | | | *Hordeum caespitosum.*[1] |
| | | | *Hordeum jubatum.*[1] |
| | | | *Hordeum pusillum.*[1] |
| | | | *Hordeum spontaneum.*[2] |
| | | | *Hordeum vulgare.*[1] |
| | | | *Hordeum vulgare (abyssinian).*[2] |
| | | | *Hordeum vulgare pallidum.*[2] |
| | | | *Hordeum vulgare pallidum pyramidatum.*[2] |
| | | | *Hystrix patula.*[1] |
| | | | *Secale cereale.*[1, 3] |
| SPECIALIZED RACE *Tritici compacti* | | | |
| | | | *Triticum compactum.*[1] |
| | | | *Triticum dicoccum.*[3] |
| | | | *Triticum durum.*[4] |
| | | | *Triticum monococcum.*[2] |
| | | | *Triticum vulgare.*[4] |
| | | | *Agropyron cristatum.*[2] |
| | | | *Agropyron desertorum.*[3] |
| | | | *Agropyron elongatum.*[2] |
| | | | *Agropyron intermedium.*[3] |
| | | | *Agropyron repens.*[3] |

[4] Some varieties were quite susceptible while others were only slightly infected.

SPECIALIZED RACE *Tritici compacti—Continued*

| Sweden—Eriksson | Russia—Jaczewski | United States—Carleton | United States—Stakman and Piemeisel |
|---|---|---|---|
| | | | *Agropyron smithii.*[1] |
| | | | *Agropyron tenerum.*[1] |
| | | | *Bromus tectorum.*[2] |
| | | | *Elymus canadensis.*[1] |
| | | | *Elymus condensatus.*[1] |
| | | | *Elymus glaucus.*[1] |
| | | | *Elymus macounii.*[1] |
| | | | *Hordeum jubatum.*[1] |
| | | | *Hordeum vulgare.*[2] |
| | | | *Secale cereale.*[3] |
| SPECIALIZED RACE *Airae* | | | |
| *Aira bottnica.*<br>*Aira caespitosa.* | *Aira caespitosa.* | | |
| SPECIALIZED RACE *Agrostis* | | | |
| *Agrostis canina.*<br>*Agrostis stolonifera.* | *Agrostis alba.* | *Agrostis alba vulgaris.* | *Agrostis alba.*[1]<br>*Agrostis canina*[2]<br>*Agrostis stolonifera.*[1]<br>*Alopecurus geniculatus.*[2]<br>*Alopecurus pratensis.*[2]<br>*Avena sativa.*[3]<br>*Bromus tectorum.*[2]<br>*Calamagrostis canadensis.*[3]<br>*Dactylis glomerata.*[2]<br>*Holcus lanatus.*[2]<br>*Hordeum vulgare.*[3]<br>*Koeleria cristata.*[2]<br>*Secale cereale.*[3] |

| Sweden—Eriksson | Russia—Jaczewski | United States—Johnson | United States—Stakman and Piemeisel |
|---|---|---|---|
| **Specialized Race *Poae*** | | | |
| *Poa caesia.*<br>*Poa compressa.*<br>*Poa pratensis.* | *Poa compressa.*<br>*Poa pratensis.*<br>*Poa serotina.* | | |
| **Specialized Race *Calamagrostis*** | | | |
| | *Calamagrostis epigeios.* | | |
| **Specialized Race *Aperae*** | | | |
| | *Apera spica venti.* | | |
| **Specialized Race *Arrhenatheri*** | | | |
| | *Arrhenatherum elatius.*<br>*Avena sativa.* | | |
| **Specialized Race *Phlei-pratensis*** | | | |
| *Phleum pratense.*<br>*Avena sativa.*<br>*Festuca elatior.*<br>*Secale cereale.* | | *Phleum pratense.*<br>*Avena sativa.*<br>*Arrhenatherum elatius.*<br>*Dactylis glomerata.*<br>*Festuca elatior.*<br>*Poa compressa.*<br>*Secale cereale.* | *Phleum pratense.*[1]<br>*Alopecurus geniculatus.*[2]<br>*Alopecurus pratensis.*[2]<br>*Arrhenatherum elatius.*[3]<br>*Avena fatua.*[3]<br>*Avena sativa.*[3]<br>*Bromus tectorum.*[3]<br>*Dactylis glomerata.*[1]<br>*Elymus virginicus.*[3]<br>*Festuca elatior.*[1]<br>*Festuca pratensis.*[1]<br>*Holcus lanatus.*[2]<br>*Hordeum jubatum.*[3]<br>*Hordeum vulgare.*[3]<br>*Koeleria cristata.*[1]<br>*Lolium italicum.*[3]<br>*Lolium perenne.*[3]<br>*Secale cereale.*[3] |

According to the various workers the specialized race *Avenae* occurs on a wide range of hosts. Eriksson (41) lists it on twenty species belonging to fourteen genera; Jaczewski (68) lists it on seven species belonging to six genera; Carleton (25) records it on nineteen species belonging to fifteen genera; Stakman and Piemeisel (149) record it on thirty-three species belonging to twenty-one genera. The specialized race *Tritici* is reported by Carleton on seventeen species belonging to seven genera; Stakman and Piemeisel list it on thirty-three species belonging to nine genera; Jaczewski lists it on six species belonging to five genera; Eriksson records it on the four cereals and states that this race seems less sharply fixed in its host relations than any of the others. Stakman and Piemeisel report another race, *Tritici compacti*, from the Palouse wheat region of western United States. This race is reported on twenty species belonging to six genera. The specialized race *Secalis* also occurs on a number of hosts, Eriksson reporting it on eleven species belonging to five genera, Jaczewski reporting it on six species belonging to four genera and Stakman and Piemeisel recording it on twenty-three species belonging to nine genera. According to Eriksson, Jaczewski and Carleton the specialized race *Agrostis* occurs only on species of *Agrostis*, while Stakman and Piemeisel report it on thirteen species of grasses belonging to ten genera. The specialized race *Arrhenatheri* occurs on both *Avena sativa* and *Arrhenatherum elatius*. The races *Airae*, *Poae*, *Calamagrostis* and *Aperae* are limited to species of a single genus.

Eriksson and Henning (43) separated the timothy rust from the black-stem rust and made it a distinct species, *Puccinia Phlei-pratensis*. The separation was based largely on the fact that they were unable, with one doubtful exception, to infect the barberry with teleutospores from timothy. Other workers have made similar attempts but without success. Stakman and Piemeisel consider it best to regard timothy rust as a race of *Puccinia graminis*.

Eriksson (34) reports successful inoculations with uredospores from timothy on *Avena sativa*, *Festuca elatior* and *Secale cereale*, negative results being obtained with *Triticum vulgare* and *Hordeum vulgare*. Johnson (69) transferred timothy rust, using uredospores, to *Avena sativa*, *Arrhenatherum elatius*, *Dactylis glomerata*, *Festuca elatior*, *Poa compressa* and *Secale cereale*. Inoculations on thirteen other grasses, including *Triticum vulgare* and *Hordeum vulgare*, gave negative results. Stakman and Piemeisel (149), however, were able to infect eighteen species of grasses belonging to thirteen genera, these including *Avena sativa*, *Hordeum vulgare* and *Secale cereale*, but not *Triticum vulgare*. They regard this race as being closely related to the race *Avenae*.

It may also be noted that Eriksson lists barley (*Hordeum vulgare*)

and rye (*Secale cereale*) as hosts for the same specialized race *Secalis*. Carleton, on the other hand, places wheat and barley as common hosts for the race *Tritici*, although he gives no information regarding the relation of the rye rust to the other forms. Other variations in the hosts for the different races, as reported by these three workers, also occur. Eriksson lists *Dactylis glomerata* as a host for the race *Avenae;* Jaczewski lists it for the race *Secalis;* and Carleton records it as a host for both races *Avenae* and *Tritici*. *Agropyron repens* is a host for the two races *Secalis* and *Tritici* according to Jaczewski. Carleton records the race *Avenae* on *Hordeum murinum*, while Eriksson places this host, along with the other species of *Hordeum*, as a host for the race *Secalis*.

It is important to note that many grasses are listed by Stakman and Piemeisel as common hosts for several races. They suggest that the six races which they experimented with may be divided into two groups on the basis of their parasitism. The races *Tritici*, *Tritici compacti* and *Secalis* form one group; these vary in their capacity for infecting certain hosts but all three vigorously infect *Agropyron cristatum*, *A. elongatum*, *A. smithii*, *Bromus tectorum*, *Hordeum jubatum*, *H. vulgare*, *Elymus canadensis* and *Hystrix patula*. The other three races, *Agrostis*, *Avenae* and *Phleipratensis*, also vary in their infecting capacity but all vigorously attack *Alopecurus geniculatus*, *A. pratensis*, *Dactylis glomerata*, *Holcus lanatus* and *Koeleria cristata*. Three hosts, *Bromus tectorum*, *Hordeum vulgare* and *Secale cereale*, are infected by all six races.

Stakman and Piemeisel do not regard the barley rust as a distinct race. Barley is a very favorable host for races *Secalis*, *Tritici*, and *Tritici compacti*, as well as being susceptible to the other three races. In the field barley seems especially to harbor the race *Tritici*.

Freeman and Johnson (57) have confined their work almost exclusively to the cereal hosts of *Puccinia graminis*. They conclude that their experiments indicate the existence of four specialized races: *Tritici* on wheat, *Hordei* on barley, *Secalis* on rye, and *Avenae* on oats. The rust on wheat can be transferred to barley and rye, but not to oats; the rust on barley can be transferred to the other three cereals, rye, oats and wheat; the rust on rye can be transferred to barley, but not to wheat nor oats; the rust on oats can be transferred to barley. These workers also report that *Hordeum jubatum* can be infected with the rust of both wheat and barley; *Agropyron repens* with the rust of wheat; and *Dactylis glomerata* with the rust of oats. So far as the cereals are concerned it appears that the different grains may be hosts for more than one specialized race of the black-stem rust. Stakman and Piemeisel, however, do not regard *Hordei* as distinct from *Tritici*.

Stakman's (143) results with the cereal rusts, in general, confirm those of Freeman and Johnson. He found that uredospores from barley infected rye, barley and wheat, but not oats; uredospores from oats infected wheat, rye and oats, but not barley; uredospores from rye infected rye, but not wheat nor barley; uredospores from wheat infected barley, rye and wheat, but not oats. Uredospores from *Agropyron repens* gave the following results: on wheat, on oats, on barley and on rye.

Stakman (144) briefly mentions some other results with this rust. He states that uredospores from *Agropyron repens*, *A. tenerum*, *A. caninum*, *A. smithii* and *Hordeum jubatum* readily infect barley and rye, very slightly wheat and practically fail to infect oats. Uredospores from *Dactylis glomerata* and *Poa nemoralis* infect oats, but not the other cereals. Practically no success was attained in trying to infect any of the cereals with uredospores from *Agrostis alba*, *A. stolonifera*, *Anthoxanthum odoratum*, *Calamagrostis canadensis*, *Poa pratensis* and *P. compressa*.

Bolley and Pritchard (20) state that uredospores from barley (*Hordeum jubatum*) and *Avena fatua* were able to infect wheat and uredospores from wheat produced infection on barley and *Hordeum jubatum*.

Pritchard (110), in North Dakota, suggests that distinct races occur on wheat and barley, although he gives no experimental evidence. Another race occurs on rye, oats, *Avena fatua*, *Agropyron repens*, *A. tenerum* and *Hordeum jubatum*, as indicated by inoculations with uredospores from the gramineous hosts and aecidiospores from the barberry.

Gassner (58) has reported brief results on this rust in South America. He was able to infect wheat with uredospores taken from barley, oats, rye, *Lolium temulentum* and *Dactylis glomerata*. Barley was also infected by uredospores from wheat.

As noted before, the infecting capacity of aecidiospores from barberry has been tested, as well as that of the uredospores from various gramineous hosts. Eriksson (41) has infected the barberry with teleutospores from more than fifty different grasses. In some cases the aecidiospores thus experimentally produced were used to inoculate various grasses. In general, the aecidiospores from the barberry are restricted in their ability to infect grasses in the same way as uredospores from the grasses which were used as a source for the teleutospores for inoculating the barberry. It should be noted, however, that aecidiospores from the barberry, produced by inoculation with teleutospores from *Bromus madritensis*, *Briza maxima*, *Festuca myurus* and *Phalaris canariensis*, recorded as hosts for the specialized race

*Avenae*, infected *Secale cereale* as well as *Avena sativa*. Eriksson, however, gives no information regarding the infecting capacity of uredospores from the four grasses mentioned.

Jaczewski (68) made fairly complete tests with aecidiospores from the barberry, obtained by inoculation with teleutospores from various gramineous hosts. He records exact correspondence between the results obtained with the aecidiospores and uredospores from the grasses used as a source for the teleutosporic infections of the barberry.

Pritchard (110) found that aecidiospores from barberry in the open infected *Avena sativa*, *A. fatua*, *Agropyron tenerum*, *A. repens*, *Hordeum jubatum* and *Secale cereale*, but not *Hordeum vulgare* nor *Triticum vulgare*. They thus correspond to the infecting capacity of uredospores from the gramineous hosts.

Stakman's (143) results are in harmony with those mentioned. In one trial, the barberry was infected with teleutospores from wheat, although standing in the open. The aecidiospores, when inoculated onto various plants, infected the following: wheat, barley, oats, rye and *Triticum monococcum*. In another test, aecidiospores from the barberry, produced by inoculation with teleutospores from *Agropyron repens*, infected wheat, barley, and rye, but not oats, while a similar series, starting with teleutospores from wheat, infected wheat, barley, rye, but not oats. These results are in close correspondence to those previously mentioned for uredospores.

Arthur (7, 8, 10) has infected the barberry with teleutospores from *Agrostis alba;* the aecidiospores produced infected *Hordeum vulgare* and *Triticum vulgare* but not *Avena sativa*. Teleutospores from *Elymus canadensis* also infected the barberry but the aecidiospores developed failed to infect *Secale cereale* and *Triticum vulgare*. Other results of Arthur are the following: aecidiospores from barberry, arising from inoculation with teleutospores from *Agropyron tenerum*, infected *Avena sativa* and aecidiospores, arising from inoculation with teleutospores from *Sitanion longifolium*, infected *Triticum vulgare*.

Freeman and Johnson (57) studied the variations in the size and shape of the uredospores of the different races. While the uredospores of the same race varied considerably in these points, yet they found well-defined differences in the uredospores of the various races. Stakman and Piemeisel have made similar studies and confirm the conclusions of Freeman and Johnson.

**Puccinia coronata** Corda. Next to *Puccinia graminis* the crown rust of grasses has been the most extensively investigated rust from the standpoint of its heteroecism and its restriction to hosts. De-Bary (17) first established the fact that the aecidial stage of a crown rust on grasses occurred on *Rhamnus*. Plowright (108) seems to have

been the first to suggest that the aecidial stage of the rust on *Rhamnus cathartica* and *Rh. Frangula* belonged to two different groups of gramineous hosts. This supposition was later confirmed by Eriksson (34, 37, 42), Klebahn (77–81, 90) and Mühlethaler (101, 102). These same workers have further discovered the existence of races of the rust on the groups of grasses which have their aecidial hosts on different species of *Rhamnus*. The specialization of *Puccinia coronata* Corda has been found to be as follows:

I. Specialized Races with their Aecidial Stage on *Rhamnus cathartica, Rh. utilis, Rh. dahurica, Rh. saxatilis* and *Rh. Imeretina* (*Puccinia coronifera* Kleb.)

1. *Avenae* on *Avena sativa* and *A. brevis.*
2. *Alopecuri* on *Alopecurus pratensis, A. arundinaceus* and, to some extent, on *Avena sativa.*
3. *Festucae* on *Festuca arundinacea, F. elatior, F. gigantea, F. varia* and *F. alpina.*
4. *Lolii* on *Lolium remotum* var. *aristatum, L. perenne, L. rigidum, L. temulentum, L. italicum, Festuca elatior* and *Holcus lanatus.*
5. *Glyceriae* on *Glyceria aquatica.*
6. *Agropyri* on *Agropyron repens.*
7. *Epigaei* on *Calamagrostis epigeios* and to some extent on *Avena sativa.*
8. *Holci* on *Holcus lanatus* and *Lolium perenne.*
9. *Bromi* on *Bromus erectus, B. erectus* var. *condensatus, B. inermis, B. secalinus, B. sterilis, B. tectorum, B. commutatus* and probably *B. asper.*
10. *Arrhenatheri* on *Arrhenatherum elatius.*

II. Specialized Races with their Aecidial Stage on *Rhamnus Frangula, Rh. Purshiana, Rh. Alaternus, Rh. californica* and *Rh. Imeretina* (*Puccinia coronata* (Corda) Kleb.)

1. *Calamagrostis* on *Calamagrostis arundinacea, C. lanceolata, C. phragmitoides, C. calybea* and *Phalaris arundinacea.*
2. *Phalaridis* on *Phalaris arundinacea, Calamagrostis arundinacea* and *C. lanceolata.*
3. *Agrostis* on *Agrostis vulgaris* and *A. stolonifera.*
4. *Holci* on *Holcus lanatus* and *H. mollis.*
5. *Agropyri* on *Agropyron repens.*

III. Race with its Aecidial Stage on *Rhamnus alpina, Rh. pumila, Rh. Imeretina* and *Rh. Purshiana* (*Puccinia alpinae-coronata* Mühlethaler)

*Calamagrostis* on *Calamagrostis varia* and *C. tenella.*

IV. Race with its Aecidial Stage on *Rhamnus dahurica* (*Puccinia himalensis* (Barclay) Diet.)

*Brachypodii* on *Brachypodium silvaticum.*

V. Race whose Aecidial Stage is Unknown

*Melicae* on *Melica nutans.*

It will be noted that the specialized races of groups I, II, and III have *Rhamnus Imeretina* as a common aecidial host. *Rhamnus Pursbiana* also occurs as an aecidial host for races of groups II and III. It also appears that specialized races on *Holcus* and *Agropyron* occur in both groups I and II. In connection with the gramineous hosts certain specialized races also overlap. For example, *Avena sativa* is a host for specialized races *Avenae*, *Alopecuri* and *Epigaei* (Group I); *Festuca elatior* is a host for specialized races *Lolii* and *Festucae* (Group I); *Calamagrostis arundinacea*, *C. lanceolata* and *Phalaris arundinacea* are hosts for specialized races *Calamagrostis* and *Phalaridis* (Group II).

Carleton (26), in this country, has tested the host relations of the crown rust on oats. He finds that the rust on *Avena sativa* can be transferred to *Avena sativa patula*, *A. sativa orientalis*, *A. sativa nuda*, *A. fatua*, *A. pratensis*, *Alopecurus alpestris*, *Phleum pratense*, *Ph. asperum*, *Dactylis glomerata*, *Aira caespitosa*, *Holcus mollis*, *Eatonia* sp. indet., *Koeleria cristata*, *Anthoxanthum odoratum*, *Festuca* sp. indet., *Phalaris arundinacea*, *Polypogon monspeliensis*, *Trisetum subspicatum*, *Brizopyron siculum* and *Poa annua*. Carleton also transferred the rust from *Phalaris caroliniana* to *Avena sativa* and *Dactylis glomerata*. The rust on *Arrhenatherum elatius* was also transferred to *Avena sativa*. Aecidiospores from *Rhamnus lanceolata* readily infected *Phalaris caroliniana* and *Avena sativa*.

Arthur (6, 11, 14) reports the successful infection of *Avena sativa* with aecidiospores from *Rhamnus lanceolata*, *Rh. caroliniana* and *Rh. cathartica*. He also succeeded in infecting *Rhamnus alnifolia* with teleutospores from *Calamagrostis canadensis*. Teleutospores from *Holcus lanatus* and *Scolochloa festucacea* failed to infect *Rhamnus cathartica*.

Treboux (159, 160) reports the results of experiments with the crown rust carried out in southern Russia which are quite at variance with those obtained in Europe. He finds that aecidiospores from *Rhamnus cathartica* obtained from a common source infected fifty-one species of grasses belonging to the genera *Alopecurus*, *Agropyron*, *Agrostis*, *Aira*, *Arrhenatherum*, *Avena*, *Brachypodium*, *Briza*, *Bromus*, *Calamagrostis*, *Dactylis*, *Eatonia*, *Festuca*, *Glyceria*, *Hierchloa*, *Holcus*, *Hordeum*, *Koeleria*, *Lolium*, *Melica*, *Phalaris*, *Poa*, *Phleum*, *Polypogon*, *Sclerochloa*, *Secale*, *Sesleria* and *Triticum*. In these experiments with *Puccinia coronifera* Kleb., Treboux obtained positive results with three hosts of *P. coronata* (Corda) Kleb.—*Agrostis stolonifera*, *Calamagrostis arundinacea* and *Phalaris arundinacea*. Treboux has also used the aecidiospores from *Rhamnus Frangula* to successfully infect nine species of grasses, among them *Avena sativa*, a host belonging to *P. coronifera* Kleb. Treboux's tests with uredospores show the

same lack of specialization to particular hosts as Carleton reports for the crown rust in the United States.

**Puccinia glumarum** (Schm.) Eriks. and Henn. Eriksson (34) is the only investigator to report on the host relations of this rust. He claims the existence of five specialized races:

1. *Tritici* on *Triticum vulgare.*
2. *Secalis* on *Secale cereale* and *Triticum vulgare.*
3. *Elymi* on *Elymus arenarius.*
4. *Agropyri* on *Agropyron repens.*
5. *Hordei* on *Hordeum vulgare.*

**Puccinia dispersa** Eriks. and Henn. Ericksson (34, 40) first separated the hosts of this rust into five distinct groups each supporting a distinct specialized race. Later each race was raised to specific rank, based on the host relations and life history.

1. *Secalis* on *Secale cereale.* This race has its aecidial stage on different species of *Anchusa.*
2. *Agropyri* on *Agropyron repens* (*Puccinia agropyrina* Eriks.). Aecidial host unknown.
3. *Bromi* on *Bromus* species (*Puccinia bromina* Eriks.). According to Müller (99), this race has its aecidial stage on *Pulmonaria montana* and *Symphytum officinalis.*
4. *Tritici* on *Triticum vulgare* (*Puccinia triticina* Eriks.). Aecidial host unknown.
5. *Holci* on *Holcus lanatus* and *H. mollis* (*Puccinia holcina* Eriks.). Aecidial host unknown.
6. *Triseti* on *Trisetum flavescens* (*Puccinia Triseti* Eriks.). Aecidial host unknown.

Müller, Ward, and Freeman have studied the rust of the bromes. Müller (103) found that aecidiospores from *Pulmonaria montana* infected *Bromus arvensis, B. brachystachys, B. erectus, B. mollis* and *B. secalinus.* Aecidiospores from *Symphytum officinalis* also infected these species of *Bromus* and, in addition, *B. brizaeformis.* Müller obtained the following results with uredospores: (1) uredospores from *Bromus erectus* infected *B. arvensis, B. brachystachys, B. erectus, B. macrostachys* and *B. mollis;* (2) uredospores from *B. arvensis* infected *B. arvensis, B. brachystachys, B. inermis* and *B. mollis;* (3) uredospores from *B. mollis* infected *B. brachystachys, B. macrostachys* and *B. mollis.*

Ward (171, 172) has carried out a large series of experiments with this rust. In his inoculation tests he used species of *Bromus* belonging to each of the five recognized subdivisions of the genus. Uredospores from eleven different species, belonging to three different sections of the genus, were used. Ward found marked differences in the susceptibility of the bromes to the uredospores from different hosts. In

general, he concludes that species of the same section of the genus as the one serving as a source of uredospores were more fully infected than the species of other sections. The evidence for Ward's conclusion is not very striking except in the case of the two hosts *Bromus mollis* and *B. sterilis*. Some of Ward's data may be indicated as follows:

| Host Inoculated | Source of Uredospores | | | | | |
|---|---|---|---|---|---|---|
| | *Bromus arvensis* | *Bromus brizaeformis* | *Bromus mollis* | *Bromus secalinus* | *Bromus arduennensis* | *Bromus sterilis* |
| *Serrafalcus:* | | | | | | |
| *Bromus arvensis* | 12/13[5] | 10/9 | 33/97 | 6/8 | | |
| *Bromus brachystachys* | 13/14 | 14/14 | 7/7 | | | |
| *Bromus brizaeformis* | 7/17 | 7/15 | 14/25 | 3/5 | | |
| *Bromus Krausei* | | | 21/27 | | | 14/59 |
| *Bromus macrostachys* | 14/15 | 16/17 | 5/19 | 5/5 | | |
| *Bromus molliformis* | | | 2/6 | | | 1/25 |
| *Bromus mollis* | 8/15 | 21/26 | 119/154 | 3/8 | 1/8 | 1/137 |
| *Bromus pendulinus* | 8/6 | 43/40 | 30/50 | | | 17/65 |
| *Bromus secalinus* | 14/14 | 14/15 | 31/61 | 16/16 | 8/8 | |
| *Bromus vestitus* | | | 3/4 | | | 1/4 |
| *Libertia:* | | | | | | |
| *Bromus arduennensis* | | | 13/14 | | 8/7 | |
| *Stenobromus:* | | | | | | |
| *Bromus gussoni* | | 10/26 | 6/53 | | | 37/60 |
| *Bromus madritensis* | | 11/13 | | 1/13 | | 43/68 |
| *Bromus maximus* | | | 1/74 | | | 2/82 |
| *Bromus sterilis* | | | 4/148 | | | 126/146 |

Freeman (56) has made a further study of the brome rust, using uredospores from *Bromus mollis* and *B. sterilis*. He states that twenty-two different species of *Bromus* remained free from infection following inoculation with rust from both hosts. Eleven species were infected with uredospores from *B. mollis* but not with uredospores from *B. sterilis*. Only one host, *B. sterilis*, was infected by uredospores from *B. sterilis*, and not by uredospores from *B. mollis*. Five species were infected with spores from both grasses.

**Puccinia Stipina** Tranzschel. Under this name, Tranzschel (156) groups the North American rust *Puccinia Stipae* Arth., with uredo and teleuto on *Stipa spartea* and aecidial stage on *Aster ericoides*, *A. multiflorus*, *A. Novae-angliae* and *Solidago canadensis*, and the European rust, *Puccinia Stipae* Bubák, with uredo and teleuto stages on *Stipa capillata* and aecidial stage on *Thymus* and *Salvia*. Klebahn (87, 91) finds evidence for two specialized races in the European rust:

[5] The denominator indicates the number of leaves inoculated and the numerator the number infected.

1. *Thymi-Stipae* Kleb.; aecidial stage on *Thymus serpyphyllum, T. angustifolius* and *T. vulgaris.*
2. *Salviae-Stipae* Kleb.; aecidial stage on *Salvia silvestris* and *S. pratensis.*

**Puccinia sessilis** Schneid. This rust, which has its uredo and teleuto stages on *Phalaris arundinacea* and its aecidial stage on various plants of the Liliaceae, Amaryllidaceae, Araceae and Orchidaceae, has been broken up into a number of distinct species, based largely upon the choice of the aecidial host. Klebahn (77–83, 86, 87, 89–91) has carried out the cultural tests with the rust and recognizes the following relations:

1. *Puccinia Smilacearum-Digraphidis* (Sopp.) Kleb.
   a. *Smilacearum-Digraphidis typica* Kleb.; aecidial stage on *Convallaria majalis, Maianthemum bifolium, Polygonatum multiflorum, P. officinale, P. verticillatum* and *Paris quadrifolia.*
   b. *Convallariae-Digraphidis* (Sopp.) Kleb.; aecidial stage on *Convallaria majalis.*
   c. *Paridi-Digraphidis* (Plowr.) Kleb.; aecidial stage on *Paris quadrifolia.*
2. *Puccinia Allii-Phalaridis* Kleb.; aecidial stage on *Allium ursinum.*
3. *Puccinia Orchidearum-Phalaridis* Kleb.; aecidial stage on *Gymnadenia conopea, Listera ovata, Orchis maculata, O. latifolia, Platanthera bifolia* and *P. Chlorantha.*
4. *Puccinia Ari-Phalaridis* (Plowr.) Kleb.; aecidial stage on *Arum maculatum.*
5. *Puccinia Schmidtiana* Diet.; aecidial stage on *Leucojum aestivum* and *L. vernum.*

It may be especially noted that, according to Klebahn, *Puccinia Smilacearum-Digraphidis* includes a race which occurs on a number of hosts and two races which occur on only one host. The hosts for the second two races are also hosts for the first race. It is further to be noted that the species recognized are also to be distinguished on the basis of host relations.

**Puccinia Caricis** (Schum.) Rebent. Klebahn (91) indicates the following specialization in the *Urtica-Carex* rust, the races being indicated by the choice of uredo and teleuto host:

1. *Urticae-acutae* on *Carex acuta, C. Goodenoughii,* to a less extent *C. stricta.*
2. *Urticae-hirtae* on *Carex hirta.*
3. *Urticae-acutiformis* on *Carex acutiformis, C. Kochiana,* to a less extent on *C. pseudocyperus.*
4. *Urticae-vesicariae* on *Carex vesicaria.*

Tranzschel (155) suggests the possibility of two other races, one on *Carex pallescens* and a second on *Carex vaginata.*

**Puccinia Centaureae-Caricis** Tranz. Tranzschel (155) suggests that the various *Centaurea-Carex* rusts may best be grouped under the above name. The following rusts are thus included:

1. *Puccinia Caricis-montanae* Ed. Fischer. Bandi (15) claims to have found evidence for the occurrence of specialization in this heteroecious rust which forms its uredospores and teleutospores on *Carex montana* and its aecidiospores on species of *Centaurea.* He mentions two specialized races based on the choice of aecidial host:
   *a.* On *Centaurea scabiosa.*
   *b.* On *Centaurea montana.*
2. *Puccinia tenuistipes* Rostrup; aecidial stage on *Centaurea Jacea;* uredo and teleuto stages on *Carex muricata.*
3. *Puccinia arenariicola* Plowr.; aecidial stage on *Centaurea nigra;* uredo and teleuto stages on *Carex arenaria.*
4. *Puccinia Jaceae-leporinae* Tranz.; aecidial stage on *Centaurea Jacea;* uredo and teleuto stages on *Carex leporina.*
5. *Puccinia Jacea-capillaris* Tranz.; aecidial stage on *Centaurea Jacea;* uredo and teleuto stages on *Carex capillaris.*
6. An unnamed rust with aecidial stage on *Centaurea orientalis;* uredo and teleuto stages on *Carex gynobasis.*

**Puccinia extensicola** Plowr. This name is applied to a group of rusts which have their aecidial stage on Compositae and their uredo and teleuto stages on species of *Carex.* Arthur (2, 3, 5, 6, 8, 9, 10, 11, 13) has listed a number of forms under distinct names, but later suggests that they are merely specialized races of *Puccinia extensicola.* The following rusts are regarded as belonging here:

1. *Puccinia Caricis-Erigerontis* Arth.; aecidial stage on *Erigeron annuus, E. canadensis* and *E. philadelphicus;* uredo and teleuto stages on *Carex festucacea.*
2. *Puccinia Caricis-Asteris* Arth.; aecidial stage on *Aster acuminatus, A. adscendens, A. cordifolius, A. paniculatus* and *Solidago graminifolia;* uredo and teleuto stages on *Carex festiva, C. foenea C. retrorsa, C. rosea, C. scoparia* and *C. trisperma.*
3. *Puccinia Caricis-Solidaginis* Arth.; aecidial stage on *Solidago caesia, S. canadensis, S. graminifolia, S. rigida, S. serotina* and *S. ulmifolia;* uredo and teleuto stages on *Carex Jamesii, C. scoparia, C. sparganoides* and *C. stipata.*

It is suggested that a distinct race may occur on *Carex scoparia* and *Solidago graminifolia.*

**Puccinia silvatica** Schroet. This rust is reported as having its

uredo and teleuto stages on various species of *Carex*, while the aecidial stage occurs on *Taraxacum officinalis*, *Crepis biennis*, *Lappa officinalis* and three species of *Senecio*. Schroeter (137) proved that the aecidium on *Taraxacum* was connected with the rust on *Carex brizoides* and *C. praecox*. Later he connected the aecidium on *Senecio nemorensis* with the rust on *Carex brizoides*. Dietel (27) connected the aecidium on *Lappa* with the *Carex* rust and Juel (72) and Bubák (24) established the connection between the aecidium on *Crepis* and the *Puccinia* on *Carex*. Wagner (167, 169), however, claims that a particular collection of teleutospores from *Carex* would not infect *Taraxacum*, *Lappa* and *Senecio* but only one of these aecidial hosts. Some collections of teleutospores infect one aecidial host while other collections infect a still different aecidial host. There is an indication, then, of a specialization to particular hosts in this rust.

**Puccinia Ribesii-Caricis** Kleb. This rust has its aecidial stage on species of *Ribes* and its uredo and teleuto stages on various species of *Carex*. Arthur (2, 4, 5, 6, 7, 8, 11, 13, 14), in this country, has carried out inoculation tests with the *Ribes-Carex* rust for a number of years. He finds that the aecidial hosts include *Ribes aureum*, *R. Cynosbati*, *R. gracile*, *R. prostratum*, *R. rotundifolium* and *R. uva-crispa;* other species not infected are *R. floridum*, *R. oxyacanthoides* and *R. rubrum*. Teleutospores were used from *Carex arctata*, *C. crinita*, *C. debilis*, *C. gracillima*, *C. intumescens*, *C. pallescens*, *C. pubescens*, *C. squarrosa*, *C. tenuis*, and *C. tetanica*. Fraser (55) reports the successful infection of *Ribes oxyacanthoides* with teleutospores from *Carex arctata* and *Carex crinita*. There appears to be no indication of the existence of specialized races.

In Europe, Klebahn (87, 91) has extensively studied the *Ribes-Carex* rust and finds evidence for the existence of five specialized races. The specialization occurs very largely in the choice of the uredo and teleuto host, as all the races pass over to practically the same species of *Ribes* as aecidial hosts. Klebahn distinguishes the following on the basis of cultural tests:

1. *Puccinia Pringsheimiana* Kleb.; uredo and teleuto tages on *Carex acuta*, *C. caespitosa*, *C. Goodenoughii*, and *C. stricta;* aecidial stage on *Ribes alpinum*, *R. aureum*, *R. Grossularia*, *R. rubrum* and *R. sanguineum*.
2. *Puccinia Ribesii-Pseudocyperi* Kleb.; uredo and teleuto stages on *Carex pseudocyperus;* aecidial stage on *Ribes alpinum*, *R. aureum*, *R. Grossularia*, *R. nigrum*, *R. rubrum* and *R. sanguineum*.
3. *Puccinia Ribis nigri-Paniculatae* Kleb.; uredo and teleuto stages on *Carex paniculata* and *C. paradoxa;* aecidial stage on *R. alpinum*, *R. aureum*, *R. nigrum*, *R. rubrum* and *R. sanguineum*.

4. *Puccinia Magnusii* Kleb.; uredo and teleuto stages on *Carex acutiformis* and *C. riparia;* aecidial stage on *Ribes alpinum, R. aureum, R. nigrum* and *R. sanguineum.*
5. *Puccinia Ribis nigri-acutae* Kleb.; uredo and teleuto stages on *Carex acuta* and *C. stricta;* aecidial stage on *Ribes alpinum, R. aureum, R. nigrum* and *R. sanguineum.*

**Puccinia Bistortae** (Str.) DC. This rust has its uredo and teleuto stages on species of *Polygonum* and its aecidial stage on various umbellifers. It is broken up into distinct races based upon the choice of the aecidial host. By some, these races are regarded as true species. According to Klebahn (91) they are as follows:

1. *Puccinia Angelicae-Bistortae* Kleb. with the aecidial stage on *Angelica silvestris* and *Carum carvi.*
2. *Puccinia Conopodii-Bistortae* Kleb. with the aecidial stage on *Conopodium denudatum.*

**Puccinia mammillata** Schroet. This rust, also with its uredo and teleuto stages on *Polygonum*, as a result of the work of Bubák (21) and Semadeni (140), is separable into two races:

1. *Puccinia Angelicae-mammillata* Kleb. with the aecidial stage on *Angelica silvestris* (*Aecidium Bubakianum* Juel).
2. *Puccinia Mei-mammillata* Semadeni with the aecidial stage on *Meum mutellina.*

**Puccinia Polygoni-amphibii** Pers. Several workers claim the existence of at least two rusts on the various species of *Polygonum* on the basis of minor morphological characteristics. *Puccinia Polygoni-amphibii* Pers. is recorded on *Polygonum amphibium* and *P. Polygoni-Convolvuli* DC. on *Polygonum convolvulus.* P. and H. Sydow (151) in their monograph of the rusts, however, claim that the differences are not sufficient to distinguish the species and consequently list the various *Polygonums* as hosts for the one rust, *Puccinia Polygoni-amphibii.*

Tranzschel (152, 153) first demonstrated the heteroecism of this *Polygonum* rust, connecting the uredo and teleuto stages on *Polygonum amphibium* with the aecidial stage on *Geranium palustre* and *G. pratense.* He further found that the uredo and teleuto stages on *Polygonum convolvulus* was connected with the aecidial stage on *Geranium pusillum.* A number of other workers have confirmed the connection between the uredo and teleuto stages on *Polygonum* and the aecidial stage on *Geranium.*

Jacob (66, 67) has carried out the most extensive series of cultural experiments with the *Polygonum* rust, using teleutospores from *Polygonum amphibium, P. convolvulus* and *P. dumetorum.* The aecidiospores produced experimentally on the various species of *Geranium,*

and also uredospores produced by aecidiosporic inoculations were also used. As the result of the experiments, Jacob concludes that the rusts on *Polygonum amphibium* and on *P. convolvulus* and *P. dumetorum* are distinct. The relationship of these two forms may be indicated as follows:

1. *Puccinia Polygoni-amphibii* Pers.; aecidial stage on *Geranium albanum*, *G. columbinum*, *G. dissectum*, *G. lucidum*, *G. molle*, *G. nodosum*, *G. pratense*, *G. pusillum*, *G. pyrenaicum*, *G. rivulare*, *G. rotundifolium* and *G. sanguineum;* uredo and teleuto stages on *Polygonum amphibium.*
2. *Puccinia Polygoni* Alb. et Schw. (*P. Polygoni-Convolvuli* DC.); aecidial stage on *Geranium columbinum*, *G. dissectum*, *G. molle*, *G. pusillum*, and *G. rotundifolium;* uredo and teleuto stages on *Polygonum convolvulus* and *P. dumetorum.*

It may be noted that the same species of *Geranium* occur as hosts for both races, although the host list for *Puccinia Polygoni-amphibii* includes more species than the other.

**Puccinia absinthii** DC. Klebahn (91) suggests the probability of specialized races in this rust although no cultural experiments have been carried out. He reports, however, minute differences in the spore measurements of the different forms. The following races are indicated:

1. *Absinthii* on *Artemisia absinthium.*
2. *Artemisiae* on *Artemisia vulgaris.*
3. *Abrotani* on *Artemisia abrotanum.*

**Puccinia bullata** (Pers.) Winter. This rust, according to Semadeni (135, 136), has a race specialized to *Silaus pratensis* and one to *Thysselinum palustre.*

**Puccinia carduorum** Jacky. Probst (112) recognizes three specialized races in this rust.

1. *Crispi* on *Carduus crispus* and *C. personata.*
2. *Deflorati* on *Carduus defloratus.*
3. A third race probably occurs on *Carduus nutans.*

**Puccinia Centaurea** Mart. Jacky (64) and Hasler (62) have both studied the specialization of this rust. Jacky suggested the occurrence of two specialized races: (*a*) *Jaceae* on *Centaurea Jacea* and (*b*) *Nervosae* on *C. nervosa.* Hasler separates out three rusts, making them species and finds additional host specialization in one of these. His arrangement is as follows:

1. *Puccinia Centaureae-vallesiacae* Hasler on *Centaurea vallesiaca*, *C. alba*, *C. rhenana* and, to a less extent, on *C. cyanus.*
2. *Puccinia Jaceae* Otth on *Centaurea Jacea*, *C. rhenana* and, to a less extent, on *Centaurea austriaca*, *C. Jacea* var. *longifolia*, *C. phrygia* and *C. transalpina.*

3. *Puccinia Centaureae* (Mart.) Hasler.
   a. *Scabiosae* on *Centaurea scabiosa.*
   b. *Nigrae* on *Centaurea nigra.*
   c. *Nervosae* on *Centaurea nervosa.*
   d. *Transalpinae* on *Centaurea transalpina, C. alba, C. austriaca, C. Jacea* var. *longifolia, C. nervosa, C. nigrescens* and *C. phrygia.*

**Puccinia chaerophylli** Purt. Semadeni (139, 140) claims that a race of this rust occurs on *Anthriscus silvestris* and another on *Chaerophyllum aureum.*

**Puccinia Epilobii-tetragoni** (DC.) Winter. Dietel (29) was unable to infect *Epilobium hirsutum* with aecidiospores from *E. tetragonum.* This is the only indication of specialization in this rust.

**Puccinia Geranii-silvatici** Karst. This rust has been reported on a few species of *Geranium* in widely separated localities. It occurs commonly on *Geranium silvaticum* in Europe. Its restriction to widely separated regions has led to the suggestion that the rust consists of geographically specialized races. Jacob (66, 67) has shown by cultural experiments that there is no specialization in Europe, for both *Geranium silvaticum* and *G. rotundifolium* are readily infected by teleutospores from the former.

**Puccinia Helianthi** Schw. Arthur, Kellerman, and Jacky have made inoculation tests using teleutospores of this rust. Jacky (65), using teleutospores from *Helianthus annuus*, infected *H. annuus, H. cucumerifolius*, and *H. californicus*, but failed to infect *H. maximiliani, H. multiflorus, H. rigidus, H. scaberrimus* and *H. tuberosus.*

Kellerman (74, 75) obtained negative results with teleutospores from *H. annuus* on eighteen species of *Helianthus.* His results with teleutospores from *H. ambiguus* were negative on twelve species and also negative with teleutospores from *H. decapetalus* on eight species. He found, however, that teleutospores from *H. mollis* infected *H. annuus* and *H. mollis* but not fourteen other species; teleutospores from *H. grosse-serratus* infected *H. annuus, H. decapetalus, H. giganteus, H. grosse-serratus, H. Kellermani, H. orygalus* and *H. tracheifolius*, but not *H. maximiliani* nor *H. mollis;* teleutospores from *H. tuberosus* infected only *H. annuus.*

Arthur (3, 4, 5, 6) secured the following results: (1) Teleutospores from *Helianthus mollis* infected *H. annuus, H. hirsutus, H. mollis, H. occidentalis, H. strumosus* and *H. tomentosus*, but not *H. grosse-serratus, H. Kellermani, H. laetiflorus, H. longifolius, H. orygalus* and *H. tuberosus;* (2) teleutospores from *H. grosse-serratus* infected *H. annuus, H. grosse-serratus, H. maximiliani* and *H. tomentosus* but not *H. decapetalus, H. hirsutus, H. laetiflorus, H. mollis, H. occidentalis,*

*H. orygalus*, *H. strumosus* nor *H. tuberosus;* (3) teleutospores from *H. laetiflorus* infected *H. annuus*, *H. divaricatus*, *H. Kellermani*, *H. laetiflorus*, *H. mollis*, *H. occidentalis* and *H. tomentosus*, but not *H. grosse-serratus*, *H. hirsutus*, *H. orygalus*, *H. strumosus*, nor *H. tuberosus*.

About the only conclusion that one can draw is that *H. annuus* and *H. tomentosus* are readily infected with teleutospores from a variety of hosts. The evidence for distinct specialized races is not very clear.

Tranzschel (158) states that he was able to infect *Helianthus annuus* with teleutospores from *Xanthium strumarium;* the aecidiospores produced on *Helianthus annuus* infected both *H. annuus* and *Xanthium strumarium*.

**Puccinia Hieracii** (Schum.) Mart. Jacky (64) first investigated this rust and found some evidence for specialization, distinguishing one race on *Hieracium villosum* and suggesting the possibility of several others. Probst (113), more recently, has studied the rust and has come to the conclusion that there are two subspecies, each with several specialized races. He arranges the forms as follows:

1. *Puccinia Piloselloidarum* Probst.
   - *a. Hoppeani* on *Hieracium hoppeanum*.
   - *b. Peleteriani* on *Hieracium peleterianum*.
   - *c. Pilosellae* (*a*) on *Hieracium pilosella*.
   - *d. Pilosellae* (*b*) on *Hieracium pilosella*.
   - *e. Velutini* on *Hieracium pilosella velutinum*.
   - *f. Auriculae* on *Hieracium auricula* and *H. peleterianum*.
   - *g. Floretini* on *Hieracium florentinum* var. *obscurum*.
   - *h. Ziziani* on *Hieracium bauhini*, *H. florentinum* var. *alethes*, *H. pratense* and *H. zizianum*.
2. *Puccinia Hieracii*.
   - *a. Silvatici* on *Hieracium glaucum*, *H. humile*, *H. ochroleucum*, *H. pictum*, *H. silvaticum* and *H. trebevicianum*.
   - *b. Silvatici pleiotrichi* on *Hieracium silvaticum* var. *pleiotrichum*.
   - *c. Silvatici gentili* on *Hieracium folcanum* and *H. intybaceum*.
   - *d. Schmidtii* on *Hieracium Schmidtii*, *H. humile* and *H. ochroleucum*.
   - *e. Cinerascentis* on *Hieracium cinerascens* and *H. ochroleucum*.

**Puccinia Leontodontis** Jacky. Probst (112) states that three specialized races occur in this rust:

1. *Hispidi* on *Leontodon hispidus*.
2. *Autumnalis* on *Leontodon autumnalis*.
3. *Pyrenaici* on *Leontodon pyrenaicus*.

**Puccinia petroselini** (DC.) Lindr. Semadeni (139, 140) distinguishes two specialized races of this rust, one on *Aethusa cynapium* and the other on *Petroselinum sativum*.

**Puccinia Pulsatillae** Kalchbr. Bubák (22) distinguishes the following races of this rust, basing the separation on the distribution and character of the sorus, not on cultural experiments:

1. *Concortica* on *Pulsatilla alpina* and *P. sulphurea.*
2. *Atragenicola* on *Atragene alpina.*
3. *Genuina* on *Anemone silvestris* and *Pulsatilla patens.*
4. *Pulsatillarum* on *Pulsatilla pratensis* and *P. vulgaris.*

**Puccinia Ribis** DC. Eriksson (39) distinguishes a specialized race *Rubri,* for he found that teleutospores from *Ribes rubrum* would infect this species but not *R. nigrum* nor *R. Grossularia.*

**Uromyces alchimillae** (Pers.) Lév. Fischer (53) has carried out a few experiments with this rust which tend to show the existence of a host specialization. The results reported, however, do not indicate any close correspondence between the plants infected with a particular collection of uredospores and the systematic grouping of the host plants within the genus *Alchimilla.* Fischer found that uredospores from hosts belonging to the section *Vulgares* infected plants belonging to sections *Pubescentes* and *Splendentes.*

**Uromyces caryophyllinus** (Schrank) Winter. Fischer (49–51) gives experimental evidence for the occurrence of specialized races in the carnation rust. The rust is heteroecious, the aecidial stage occurring on *Euphorbia Gerardiana* and the uredo and teleuto stages on various Caryophyllaceae. Fischer finds that aecidiospores from *Euphorbia Gerardiana* in one locality are able to infect only *Tunica prolifera,* while aecidiospores collected on the same host in another region are able to infect only *Saponaria ocymoides.* In still other localities, however, a race of rust is found that is able to infect both *Tunica* and *Saponaria.*

**Uromyces Dactylidis** Otth and **U. Poae** Rabh. These rusts, probably indistinguishable by any well-defined structural characteristics, are further alike in having their aecidial stage on species of *Ranunculus.* The former develops its uredo and teleuto stages on *Dactylis glomerata,* while the latter has the corresponding stages on several species of *Poa, Agrostis alba* also being listed as a host. A large number of workers have contributed to our knowledge concerning the heteroecism of these rusts.

Krieg (93, 94) and Klebahn (89, 91) have worked with *Uromyces Dactylidis* from the standpoint of specialization and the following races are indicated:

1. Aecidial stage on *Ranunculus bulbosus* and *R. repens.*
2. Aecidial stage on *Ranunculus lanuginosus,* to a slight extent on *R. bulbosus* (*Uromyces lanuginosi-dactylidis* Kleb.).
3. Aecidial stage on *Ranunculus aconitifolius, R. alpestris, R. glacialis,* and *R. platanifolius* (*Uromyces platanifolii-dactylidis* Krieg.).

4. Aecidial stage on *Ranunculus silvaticus* (*Uromyces silvatici-dactylidis* Krieg.).
5. Aecidial stage on *Ranunculus acer* and *R. polyanthemos.*

Juel (73) distinguishes several forms in *Uromyces Poae*:

1. *Ficariae-nemoralis* on *Ranunculus Ficaria* and *Poa nemoralis.*
2. *Ficariae-trivialis* on *Ranunculus Ficaria* and *Poa nemoralis* and *P. palustris.*
3. *Ficariae-pratensis* on *Ranunculus Ficaria* and *Poa pratensis.*
4. *Repentis-nemoralis* on *Ranunculus repens* and *R. bulbosus* and *Poa nemoralis.*
5. *Repentis-trivialis* on *Ranunculus repens* and *Poa trivialis* and *P. annua.*
6. *Auricomi-pratensis* on *Ranunculus auricomus* and *Poa pratensis* and *P. nemoralis.*
7. *Cassubici-pratensis* on *Ranunculus cassubicus* and *Poa pratensis.*
8. *Repentis-pratensis* on *Ranunculus repens* and *Poa pratensis.*
9. *Bullati-bulbosae* on *Ranunculus bullatus* and *Poa bulbosa.*

**Uromyces Fabae** (Pers.) de Bary. Jordi (70, 71) has distinguished the following specialized races on this autoecious rust which is recorded as occurring on species of *Lathyrus*, *Lens*, *Pisum*, and *Vicia*:

1. On *Lathyrus vernus* and probably on *Pisum sativum.*
2. On *Vicia Faba* and *Pisum sativum.*
3. On *Vicia cracca*, *V. hirsuta* and *Pisum sativum.*

It should be noted that *Pisum sativum* is listed as a host for all three specialized races.

**Uromyces Geranii** (DC.) Otth and Wartm., and **U. Kabatianus** Bubák. The first mentioned species is reported as occurring on a large number of different species of *Geranium*, while the second mentioned has been reported only on *Geranium pyrenaicum.* Bubák (23) has called attention to minor morphological differences between the two rusts.

Bock (19) carried out tests with uredospores of *Uromyces geranii* from *Geranium silvaticum* and was able to infect sixteen species while thirteen gave negative results. Jacob (66, 67) also conducted experiments with the rust, using teleutospores from *Geranium silvaticum* and aecidiospores produced from the teleutosporic inoculation. A considerable number of species of *Geranium* were successfully infected. A few gave negative results. Jacob also used teleutospores of *Uromyces Kabatianus* from *Geranium pyrenaicum* and found that this rust could also be transferred to a considerable number of other species of *Geranium.* The host range of the two rusts is very similar and the differences between the two depend upon minor structural differences and not on host relations.

**Uromyces Pisi** (Pers.) Winter. This rust is heteroecious forming its aecidial stage on various species of *Euphorbia* and its uredo and teleuto stages on species of *Lathyrus* and *Pisum*. The aecidial mycelium is perennial in the *Euphorbia* host. It may also be noted that aecidial stages on *Euphorbia*, especially *E. cyparissias*, have been connected with a number of different species of *Uromyces* on legumes. The aecidia belonging to these different rusts are quite indistinguishable by structural features. Jordi (70, 71) suggests that specialized races of *U. Pisi* occur on *Lathyrus pratensis* and *Vicia cracca;* the latter race is by some recognized as a species—*Uromyces Fischeri-Eduardi*.

**Uromyces proeminens** (DC.) Lév. P. and H. Sydow (151) list twenty-eight species of *Uromyces* on the species of *Euphorbia*, basing their separations largely on the studies of Tranzschel (157) in this group of rusts. Nine species are recorded as autoecious and have all four spore-forms present, the others either being short-cycled or the life history incompletely known. The structural differences between many of these species are very slight and the characters used as a basis for separation are, in many cases, quite variable. In fact Arthur (12) has grouped several of the full-cycled forms under the one species *Nigredo proeminens*, suggesting the occurrence of specialized races. Arthur (1, 2, 3) has obtained the following results with inoculation experiments: aecidiospores from *Euphorbia nutans* infected *E. nutans* but not *E. maculata*, *E. marginata* nor *E. humistrata;* aecidiospores from *E. humistrata* infected *E. humistrata* and *E. nutans* but not *E. maculata;* uredospores from *E. dentata* infected *E. dentata* but not *E. humistrata*, *E. nutans* nor *E. marginata;* uredospores from *E. nutans* infected *E. nutans* but not *E. maculata*.

Arthur (12) suggests that a race is restricted to the section *Poinsettia*, a second race to the section *Dichrophyllum*, a third race to the prostrate species, and the fourth to the more upright species of the section *Chamaesyce* of the genus *Euphorbia*.

**Uromyces Scirpi** (Cast.) Burr. This rust has its uredo and teleuto stages on *Scirpus maritimus* and its aecidial stage on *Glaux maritima*, *Hippuris vulgaris*, *Berula angustifolia*, *Daucus carota*, *Oenanthes aquatica*, *O. crocata*, *Pastinaca sativa* and *Sium latifolium* in Europe. The similar rust in this country forms its uredo and teleuto stages on *Scirpus americanus*, *S. campestris*, *S. fluviatilis* and *S. robustus*, and its aecidial stage on *Cicuta bulbifera*, *C. maculata*, *Glaux maritima*, *Oenanthes Californica* and *Sium cicutaefolium*. A good deal of experimentation has been carried on by Klebahn and others to determine the host relations of the rust and various races have been separated out as distinct species. Klebahn (89, 91) distinguishes the following:

1. *Uromyces Pastinacae-scirpi* Kleb.; aecidial stage on *Pastinaca sativa.*
2. *Uromyces Berulae-scirpi* Kleb.; aecidial stage on *Berula angustifolia.*

Dietel (28) was able to infect with teleutospores from a single host *Sium latifolium* and *Hippurus vulgaris.*

**Gymnosporangium tremelloides** Hartig. There is but little indication in the literature of the existence of specialized races in *Gymnosporangium.* Most of the species of this genus are quite restricted in host range, often occurring on only a few species of a single genus of host. Klebahn (89) gives some evidence for a host specialization of *Gymnosporangium tremelloides*, the teleutospores of which are produced on *Juniperus communis.* On the basis of cultural tests he suggests the following:

1. *Gymnosporangium Ariae-tremelloides* Kleb. Aecidial stage on *Sorbus aria* and *S. torminalis.*
2. *Gymnosporangium Mali-tremelloides* Kleb. Aecidial stage on *Pyrus malus.*

**Ochrospora Ariae** (Fuckel.) Syd. Fischer (45) stated that he was unable to infect *Aruncus silvestris* with uredospores of *Ochrospora ariae* from *Sorbus aucuparia.* Tranzschel (152, 153), Fischer (45) and Klebahn (89) showed that *Sorbus aria, S. scandica* and *Pyrus malus* were all hosts of the same race, but *Aruncus silvestris* could not be infected with spores from the same source. Later, however, Fischer (48) was able to infect *Sorbus aucuparia* and *Aruncus silvestris* with the same aecidiosporic material from *Anemone nemorosa.*

**Pucciniastrum Abieti-Chamaenerii** Kleb. and **P. Epilobii** (Pers.) Otth. These two rusts, according to Klebahn (83, 87), are distinguished almost solely on the basis of their life cycle. The former is heteroecious with its aecidial stage on *Abies balsamea* and *A. pectinata* and its uredo and teleuto stages on *Epilobium angustifolium, E. Dodonacum* and *E. latifolium.* The latter has its uredo and teleuto stages on a number of other species of *Epilobium* and its aecidial host is as yet not known.

**Phragmidium disciflorum** (Tode.) James. Bandi (15) suggests that a host specialization occurs in this rust. He reports one race on *Rosa cinnamomea, R. pimpinellifolia* and *R. rubrifolia* and a second race on *R. canina* and *R. centifolia.*

**Coleosporium Campanulae** (Pers.) Lév. This rust has its aecidial stage on *Pinus montana, P. rigida* and *P. sylvestris*, and its uredo and teleuto stages on a considerable number of different species and general of the Campanulaceae. Wagner (170) and Klebahn (87, 91) have made extensive studies with reference to the specialization of the rust on different hosts. Klebahn makes the following races:

1. *Campanulae-rapunculoides* Kleb. on *Campanula rapunculoides* and, in favorable cultures, on *C. bononiensis*, *C. glomerata*, *C. glomerata* var. *dahurica*, *C. lamiifolia*, *C. latifolia*, *C. nobilis*, *Phyteuma orbiculare* and *Ph. spicatum;* not on *Campanula rotundifolia*, nor *C. trachelium*.
2. *Campanulae-trachelii* Kleb. on *Campanula trachelium* and, in favorable cultures, on *C. bononiensis*, *C. glomerata*, *C. glomerata* var. *dahurica*, *C. latifolia* var. *macrantha*, *C. nobilis*, *C. rapunculoides* and *Wahlenbergia hederacea;* not on *Campanula pusilla*, *C. rotundifolia* nor *C. turbinata*.
3. *Campanulae-rotundifoliae* Kleb. on *Campanula rotundifolia* and, in favorable cultures, on *C. bononiensis*, *C. glomerata* var. *dahurica*, *C. pusilla*, *C. turbinata*, *Phyteuma orbiculare*, *Ph. spicatum* and *Wahlenbergia hederacea;* not on *Campanula rapunculoides* nor *C. trachelium*.

Wagner indicated the following additional races:

4. *Campanulae-Phyteumatis* Wagner on *Phyteuma spicatum*.
5. *Campanulae-macranthae* Wagner on *Campanula macrantha* (*C. latifolia* var. *macrantha*).
6. *Campanulae-patulae* Wagner on *Campanula rotundifolia* and *C. patula*.

Klebahn, however, does not believe that these can be distinguished from the first three. It may also be noted that a number of plants occur as hosts for more than one race.

**Coleosporium Senecionis** Fr. Wagner (168) first gave evidence of host specialization in this rust. Fischer (54) has also investigated the rust and the following races are indicated:

1. *Senecionis silvatici* on *Senecio silvaticus*, *S. viscosus* and *S. vulgaris* (*Senecionis* I of Wagner).
2. *Senecionis Fuchsii* on *Senecio Fuchsii* and *S. nemorensis* (*Senecionis* II of Wagner).
3. *Senecionis subalpini* on *Senecio subalpinus* (*Coleosporium subalpinum* Wagner).
4. *Senecionis doronici* on *Senecio doronicum*.

**Melampsora Euphorbiae** (Schub.) Cast. This rust, completing its life cycle on species of *Euphorbia*, has been studied by W. Müller (105, 106) who claims the existence of the following races:

1. *Euphorbiae-cyparissiae* W. Müller on *Euphorbia cyparissias*.
2. *Euphorbiae-exiguae* W. Müller on *Euphorbia exigua*.
3. *Euphorbiae-pepli* W. Müller on *Euphorbia peplus*.

**Melampsora Euphorbiae dulcis** Otth. This autoecious rust on *Euphorbia* is very similar to *Melampsora Euphorbiae*. As a result of the experimental work of W. Müller (105, 106) and Klebahn (91) two races are indicated:

1. *Euphorbiae-dulcis* s. str. on *Euphorbia dulcis.*
2. *Euphorbiae-strictae* W. Müller on *Euphorbia stricta* and *E. platyphyllos.*

**Melampsora populina** Lév. and **Melampsora Tremulae** Tul. A number of different species of *Melampsora* are recorded as having their uredo and teleuto stages on the various kinds of poplars. These rusts, however, constitute a group of closely related forms and differ but little in their structural characteristics. The main differences appear to be in the choice of hosts, especially in the aecidial stage.

The relationships between the poplar rusts may best be indicated by grouping them under the above names. *Melampsora populina* is distinguished from *M. Tremulae* by the fact that the teleutospores are subcuticular while in the case of *M. Tremulae* they are subepidermal. The uredo and teleuto hosts are also different species of *Populus* and serve further as a means of distinguishing between the two. Klebahn (87, 91) has made a special study of these rusts.

*Melampsora populina* includes two rusts which can be distinguished only by the choice of the aecidial host. These are:

1. *Melampsora Allii-populina* Kleb.; aecidial stage on *Allium cepa* and *A. ursinum;* uredo and teleuto stages on *Populus balsamifera* and *P. nigra.*
2. *Melampsora Larici-populina* Kleb.; aecidial stage on *Larix decidua;* uredo and teleuto stages on *Populus balsamifera* and *P. nigra.*

*Melampsora Tremulae* includes four or five rusts whose uredo and teleuto stages occur on *Populus alba* and *P. tremula*, rarely on other species; the aecidial stage is found on widely separated host plants. The following belong in this group:

1. *Melampsora Larici-Tremulae* Kleb.; aecidial stage on *Larix decidua.*
2. *Melampsora pinitorqua* Rostr.; aecidial stage on *Pinus silvestris.*
3. *Melampsora Rostrupii* Wagner; aecidial stage on *Mercurialis perennis.*
4. *Melampsora Magnusiana* Wagner; aecidial stage on *Chelidonium major.*
5. *Melampsora Klebahni* Bubák; aecidial stage on *Corydalis cava, C. digitata, C. fabacea, C. laxa* and *C. solida.* This may not be distinct from the preceding one.

Melampsoras of *Salix.* The Melampsoras on different species of *Salix* constitute a complex group of interrelated rusts. The structural differences between the large number of commonly recognized species are comparatively insignificant. In order to segregate the different species it is necessary to rely, to a large extent, upon differences in the choice of host. The willow rusts also afford many parallels among the poplar rusts and in some cases it is not possible to distinguish the rusts on these two genera except by the choice of host.

Klebahn (87, 91) and Schneider (133–135) have been the principal investigators of the willow rusts from the standpoint of host specialization. While many forms have been segregated out, Klebahn (92) has recently indicated the value of grouping these on the basis of structural features. The relationship of some of these different willow rusts, based upon structural characteristics and physiological specialization, may be indicated.

**Melampsora Larici epitea** Kleb. The aecidial stage occurs on *Larix decidua* and the uredo and teleuto stages on various species of *Salix*. Klebahn (87, 91) and Schneider (133–135) have carried out a number of inoculation tests and have distinguished the following races:

*a*. *Larici-epitea typica* Kleb. on *Salix aurita*, *S. cinerea*, *S. caprea*, *S. hippophaëfolia* and *S. viminalis*.

*b*. *Larici-daphnoides* Kleb. on *Salix daphnoides*.

*c*. *Larici-retusae* Ed. Fischer on *Salix retusa* and *S. herbacea*.

*d*. *Larici-nigricantis* Schneider on *Salix nigricans*, *S. glabra* and *S. hegetschweileri*.

*e*. *Larici-purpureae* Schneider on *Salix purpurea*.

*f*. *Larici-reticulatae* Schneider on *Salix reticulata* and *S. hastata*.

Klebahn states that minute structural differences can be observed in *a*, *b*, and *c*.

**Melampsora Ribesii-purpureae** Kleb. The aecidial stage occurs on species of *Ribes* and the uredo and teleuto stages on various species of *Salix*. Specialized races occur, according to Klebahn (87, 91) and Schneider (133–135), as follows:

*a*. *Ribesii-purpureae* Kleb. on *Salix purpurea* and *S. purpurea* × *S. viminalis;* to a less extent on *S. daphnoides*.

*b*. *Ribesii-auritae* Kleb. on *Salix aurita* and possibly on *S. Caprea* and *S. cinerea*.

*c*. *Ribesii-grandifoliae* Schneider on *Salix grandifolia* and *S. aurita*, and possibly on *S. arbuscula*.

Klebahn places (*a*) and (*b*) under a separate species *Melampsora Ribesii-epitea* Kleb.

**Melampsora Evonymi-Capraearum** Kleb. The aecidial stage appears on species of *Evonymus* and the uredo and teleuto stages on various species of *Salix*. Schneider (133–135) distinguishes two specialized races:

*a*. *Evonymi-capraearum typica* Schneider on *Salix aurita*, *S. Caprea*, and *S. cinerea*.

*b*. *Evonymi-incanae* Schneider on *Salix incana* and *S. caprea*, not on *S. aurita* nor *S. cinerea*.

**Melampsora Larici-pentandrae** Kleb. and **M. Salicis-albae** Kleb.

According to Klebahn (84, 87, 91), *Melampsora Larici-pentandrae* Kleb., with its aecidial stage on *Larix decidua* and uredo and teleuto stages on *Salix fragilis* and *S. pentandra*, is hardly distinguishable from *Melampsora Salicis-albae* Kleb., with its aecidial stage on species of *Allium* and its uredo and teleuto stages on *Salix alba*, except on the basis of host relations.

**Melampsora Allii-fragilis** Kleb. and **M. Galanthi-fragilis** Kleb. According to Klebahn (84, 85, 87, 91), a similar relation exists between *Melampsora Allii-fragilis* Kleb., with its aecidial stage on species of *Allium* and uredo and teleuto stages on *Salix fragilis* and *S. pentandra*, and *Melampsora Galanthi-fragilis* Kleb., with its aecidial stage on *Galanthus nivalis* and uredo and teleuto stages on the same two species of *Salix*.

**Melampsorella Caryophyllacearum** (DC.) Schroet. Bubák (24), Klebahn (87), and Fischer (45) have given some evidence for specialization in this rust. Fischer, using the same collection of aecidiospores, infected *Stellaria media*, *S. graminea*, *Arenaria serphyllifolia*. *Malachium aquaticum* and *Cerastium* sp. indet., while *Cerastium arvense*, *Moehringia trinervia* and *M. mucosa* were not infected. Klebahn obtained somewhat similar results.

**Melampsoridium betulinum** (Tul.) Kleb. Klebahn (87, 91) suggests the occurrence of at least two specialized races of this rust which has its aecidial stage on *Larix decidua* and its uredo and teleuto stages on species of *Betula*. He found that aecidiospores from *Larix*, produced by inoculation with teleutospores from *Betula pubescens*, infected *B. pubescens* and *B. nana* very abundantly and *B. verrucosa* sparingly; aecidiospores from *Larix*, produced by inoculation with teleutospores from *Betula verrucosa*, infected *B. verrucosa* abundantly, *B. nana* sparingly, and *B. pubescens* not at all. Accordingly the following races are indicated:

1. *Betulae-verrucosae* Kleb. on *Betula verrucosa* and *B. nana*.
2. *Betulae-pubescentis* Kleb. on *Betula pubescens*, *B. nana* and, to a slight extent, on *B. verrucosa*.

The above review lists the occurrence of host specialization in more than fifty different rusts. The nature of the specialization of these rusts may be indicated by arranging them in the following groups:

1. Heteroecious rusts in which the aecidial host (or hosts) is common to several specialized races which occur on the uredo and teleuto hosts: *Coleosporium Campanulae* (Pers.) Lév., *C. Senecionis* Fr., *Melampsora Evonymi-Caprearum* Kleb., *M. Larici-epitea* Kleb., *M. Ribesii-purpureae* Kleb., *Melampsorella Caryophyllacearum* Schroet., *Melampsoridium betulinum* (Tul.) Kleb.,

*Ochropsora Ariae* (Fuck.) Syd., *Puccinia graminis* Pers., *P. Caricis* (Schum.) Rebent., *P. Polygoni-amphibii* Pers., *Uromyces caryophyllinus* (Schrank) Winter, and *Uromyces Pisi* (Pers.) Winter.

Certain other rusts might also be looked for in this group as *Puccinia coronata* (Corda) Kleb., *P. lolii* Niels. (*P. coronifera* Kleb.) and *P. bromina* Eriks.

2. Heteroecious rusts in which the uredo and teleuto host (or hosts) is common to several races which occur on the aecidial hosts: *Gymnosporangium tremelloides* Hartig, *Melampsora populina* Lév., *M. Tremulae* Tul., *Puccinia Bistortae* (Str.) DC., *P. mammillata* Schroet., *P. sessilis* Schneid., *P. silvatica* Schroet., *Uromyces Dactylidis* Otth, *U. Scirpi* (Cast.) Burr.
3. Heteroecious rusts in which the specialized races are recognized by their selection of both aecidial and uredo and teleuto hosts: *Puccinia Centaureae-Caricis* Tranz., *P. coronata* Corda, *P. dispersa* Eriks. and Henn., *P. extensicola* Plowr., *P. glumarum* (Schm.) Eriks. and Henn., *P. Ribesii-Caricis* Kleb., *P. Stipina* Tranz., *Uromyces Poae* Rebent.
4. Autoecious rusts and those whose life history is incompletely known. The following belong in this group: *Melampsora Euphorbiae* (Schub.) Cast., *M. Euphorbiae-dulcis* Otth, *Phragmidium disciflorum* (Tode.) James, *Puccinia Absinthii* DC., *P. bullata* (Pers.) Winter., *P. Carduorum* Jacky, *P. Centaureae* Mart., *P. Chaerophylli* Purt., *P. Epilobii-tetragoni* (DC.) Winter., *P. Helianthi* Schw., *P. Hieracii* (Schum.) Mart., *P. Leontodontis* Jacky, *P. Petroselini* (DC.) Lindr., *P. Pulsatillae* Kalchbr., *P. Ribis* DC., *Uromyces Fabae* (Pers.) de Bary, *U. proeminens* (DC.) Lév.

### Powdery Mildews—Erysiphaceae

The first work carried on to determine whether a host specialization occurs among the species of the powdery mildews was that of Neger (107), the results of which were published in 1902. Since then a number of workers have contributed to the evidence for specialized races in this well-defined group of parasites. In fact, at the present time, one or more species of five of the six genera of the Erysiphaceae have been tested. In most cases, however, the data are very meager and it is not possible to draw any definite conclusions. In a few cases, notably for *Erysiphe graminis* and *E. cichoracearum*, the facts are better established.

**Erysiphe cichoracearum** DC. The host relations of this species was first reported upon by Neger (107) who obtained the following

results: (1) conidia from *Artemisia vulgaris*, *Lactuca muralis* and *Lithospermum arvense* infected plants of the same species but did not infect each other nor some other plants tested; (2) conidia from *Hieracium murorum* infected *H. murorum* and *Leontodon taraxacum*, the latter very slightly; (3) conidia from *Senecio vulgaris* infected *S. vulgaris* and *Lactuca muralis;* (4) conidia from *Lappa major*, *Plantago major*, *Pulmonaria officinalis* and *Verbascum thapsiforme* failed to infect any host inoculated.

Salmon (128) reports the successful infection of *Plantago major* and *P. media*, using conidia from the former; negative results were obtained with *Plantago lanceolata*, *Eupatorium cannabinum* and *Galium Aparine*.

The writer (115, 116) has carried on a very extensive series of experiments with this mildew, particularly with the cucurbit hosts. In the main, the mildew as found on the Hubbard squash (*Cucurbita maxima*) was used for inoculating the various plants. It was found that this mildew readily infected *Cucurbita maxima* (seven varieties), *C. moschata* (three varieties), *C. pepo* (seventeen varieties), *C. foetidissima*, *Cucumis dipsaceus*, *C. melo* (nine varieties), *C. sativus* (eight varieties), *Cyclanthera explodens*, *Echinocystis lobata*, *Lagenaria vulgaris* (six varieties), *Momordica charantia* and *Sicyos angulatus*. Partial infection of the following was obtained: *Citrullus vulgaris* (seven varieties), *Cucumis anguria* (two varieties), *Ecballium elaterium*, *Melothria scabra* and *Momordica balsamina*. *Coccinea cordifolia*, *Luffa acutangula* and *L. Aegyptiaca* proved to be entirely resistant. To a slight extent it was possible to transfer the cucurbit mildew to the sunflower (*Helianthus annuus*) and plantain (*Plantago rugellii*). Efforts to transfer it to *Aster cordifolius*, *A. laevis* and *Solidago caesia* failed. It was also found that a race of mildew occurred on *Aster cordifolius*, *A. laevis* and *A. sagittifolius*, not passing over to *Cucurbita maxima* nor *Solidago caesia*. Another race occurs on *Solidago caesia*, infecting this species but not passing over to asters or cucurbits.

**Erysiphe graminis** DC. Marchal (97) was the first to demonstrate host specialization in this powdery mildew. As a result of his tests he concluded that the following races may be distinguished, although he gives us no details of his evidence:

1. *Tritici* upon *Triticum vulgare*, *T. Spelta*, *T. polonicum* and *T. turgidum;* not on *T. durum*, *T. monococcum* nor *T. dicoccum*.
2. *Hordei* upon *Hordeum hexastichon*, *H. vulgare*, *H. trifurcatum*, *H. nudum*, *H. jubatum* and *H. murinum;* not on *H. maritimum*, *H. secalinum* nor *H. bulbosum*.
3. *Secalis* upon *Secale cereale* and *S. anatolicum*.
4. *Avenae* upon *Avena sativa*, *A. fatua*, *A. orientalis* and *Arrhenatherum elatius*.

5. *Poae* upon *Poa annua, P. trivialis, P. pratensis, P. caesia, P. mutalensis, P. nemoralis* and *P. serotina.*
6. *Agropyri* upon *Agropyron.*
7. *Bromi* upon various species of *Bromus.*

Salmon (123, 128) has infected *Avena nuda, A. brevis* and *A. sativa* with conidia from *A. nuda;* conidia from *A. sterilis* infected *A. pratense* and *A. sativa;* and conidia from *A. sativa* infected *A. sativa, A. brevis, A. nuda, A. orientalis, A. sterilis* and *A. strigosa.* Attempts to infect twelve other grasses, belonging to different genera, with the oat mildew failed.

The writer (120) has carried out an extensive series of experiments with the powdery mildew on *Avena sativa.* Infection occurred on the following: *A. barbata, A. brevis, A. fatua, A. fatua* var. *glabrata, A. ludoviciana, A. nuda, A. nuda* var. *chinensis, A. nuda* var. *elegantissima A. planiculmis, A. pratensis, A. pubescens, A. purpurea, A. sativa* (sixteen varieties), *A. sativa orientalis* (six varieties), *A. sterilis, A. strigosa* and *A. sulcata.* In most cases, in a large number of trials, one hundred percent of infection was secured. The oat mildew also infected *Arrhenatherum avenaceum.* Negative results were obtained with *Avena bromoides* and *A. sempervirens,* as well as grasses belonging to other genera. This race, then, extends over a wide range of species and varieties of *Avena,* but, with the exception of *Arrhenatherum avenaceum,* is restricted to this genus.

Salmon (123, 132) has reported only a few results with the powdery mildew of wheat. He successfully infected *Triticum vulgare* and *T. Spelta* with conidia from the former. He also states that young seedlings of *Hordeum silvaticum* could be infected with the same mildew.

Vavilov (164) has tested out, under field conditions, seven hundred and fifty-five "pure-lines" belonging to the different species and varieties of *Triticum.* He used pure lines belonging to thirty varieties of *Triticum vulgare,* seven of *T. compactum,* ten of *T. turgidum,* nine of *T. Spelta,* fifteen of *T. durum,* three of *T. polonicum,* five of *T. dicoccum* and four of *T. monococcum.* In general the pure lines belonging to the different varieties of *T. vulgare, T. compactum* and *T. Spelta* are extremely susceptible to the mildew, while the pure lines of the varieties of *T. durum, T. turgidum, T. polonicum* and *T. monococcum* proved, in the main, to be quite resistant. The pure lines of some varieties of *T. dicoccum* proved to be highly susceptible, while the pure lines of other varieties were markedly resistant. Differences in the susceptibility of the pure lines were noted and certain varieties, notably *T. vulgare* var. *fuliginosum* and *T. dicoccum* var. *picnurum* stood out as distinctly immune. However, the pure lines

belonging to the various varieties of all the species of *Triticum*, with the exception of certain ones, as those just noted, proved quite susceptible when they were tested under greenhouse conditions. Vavilov suggests that the greenhouse conditions are much more favorable to the development of the powdery mildew and thus more or less immune races may be successfully attacked by the fungus.

The writer (117, 118, 120) has carried on a very extensive series of tests with the powdery mildew of the wheat. One hundred and sixty-one varieties belonging to the eight recognized types or species of *Triticum* have been tested under greenhouse conditions, many tests having been made with nearly all of these. The results are summarized in the following table:

VARIETIES OF SPECIES OR TYPES OF *Triticum* IN RELATION TO THE WHEAT MILDEW

| Species of type | Varieties | 100% infection | 90–99% infection | 50–89% infection | 10–49% infection | 0–9% infection |
|---|---|---|---|---|---|---|
| *Compactum* | 6 | 2 | 1 | 2 | 1 | 0 |
| *Dicoccum*[6] | 24 | 8 | 3 | 6 | 3 | 4 |
| *Durum*[7] | 45 | 36 | 0 | 6 | 2 | 1 |
| *Monococcum* | 6 | 0 | 1 | 3 | 1 | 1 |
| *Polonicum* | 10 | 9 | 1 | 0 | 0 | 0 |
| *Spelta*[8] | 11 | 8 | 1 | 2 | 0 | 0 |
| *Turgidum* | 7 | 3 | 2 | 2 | 0 | 0 |
| *Vulgare*[9] | 52 | 35 | 5 | 6 | 3 | 3 |
| Total | 161 | 101 | 14 | 27 | 10 | 9 |

It is thus seen that the great majority of the varieties are highly susceptible to the wheat mildew. It may be specially noted that *T. dicoccoides* Kcke. the wild wheat of Palestine, proved to be quite susceptible. The distinctly resistant varieties included *T. dicoccum* var. *Khapli*, *Russian emmer* and *Spring emmer* and *T. vulgare* var. *caesium* and *pyrothrix*.

Various other species of *Triticum* have also been tested, *T. bicorne* Forsk and *T. caudatum* Gren. & Godr. proving to be highly susceptible and *T. triaristatum* Gren. & Godr. and *T. triuncinale* Rasp. proving to be resistant.

The writer (119, 120) has also found that the powdery mildew of

[6] Summary includes *Triticum Cienfuegos* Lagh., *T. dicoccoides* Kcke., *T. Freycenetii* Host., *T. Meyeri*, *T. Tumonia* Schrad. and *T. durum* Desf. var. *plenissimum*.

[7] Summary includes *T. abyssinicum* Steud. and *T. dicoccum* Schrank var. *campylodon*.

[8] Summary includes *T. Thaoudar* Reut. and *T. dicoccum* Schrank var. *cladurum*.

[9] Summary includes *T. durum* Desf. var. *africanum* and *Triticum* species indet. var. *Tibetan*.

wheat readily passes over to certain species of *Aegilops* which some systematists regard as a subgenus of *Triticum*. *Aegilops aristata*, *Aeg. Aucheri*, *Aeg. cylindrica*, *Aeg. ligustica*, *Aeg. speltoides*, *Aeg. squarrosa*, *Aeg. triaristata* and *Aeg. ventricosa* proved very susceptible, while *Aeg. ovata* and *Aeg. triticoides* gave negative results.

It is evident that the powdery mildew of wheat can successfully attack a very wide range of varieties belonging to the various species of *Triticum*. It cannot, however, pass over onto *Avena sativa*, *Hordeum vulgare*, *Secale cereale* and other grasses tested.

The powdery mildew of rye has been tested out by the writer (110); *Secale cereale*, *S. anatolicum* and *S. montanum* were readily infected, *S. dalmaticum* proving resistant. This mildew will not pass over onto any other cereal, nor such grasses as *Bromus mollis*, *Dactylis glomerata*, *Festuca elatior*, *Glyceria fluitans*, *Hordeum jubatum*, *Lolium perenne*, *Phleum pratense* and various species of *Poa*.

Treboux (161) also states that conidia from *Secale cereale* infected *S. cereale* but not *Hordeum vulgare* nor *Triticum vulgare*.

Salmon (128) reports meager data for the quack grass mildew; conidia from *Agropyron repens* infected *A. caninum* and *A. tenerum*, but not *A. repens*, *A. acutum* nor *A. glaucum*.

Salmon (128) reports the successful infection of *Poa annua*, *P. nemoralis* and *P. pratensis* with the mildew on the latter. The writer (110) has successfully used the mildew on *P. pratensis* to infect *P. compressa*, *P. nemoralis*, *P. pratensis* and *P. trivialis*. A number of other grasses tested by these workers have given negative results.

The powdery mildew of barley has been tested by both Salmon (125) and the writer (117). According to the former the mildew from *Hordeum vulgare* is readily transferred to *H. decipiens*, *H. distichon*, *H. hexastichon*, *H. intermedium*, *H. vulgare* and *H. zeocriton*, while it is not transferable to *H. jubatum*, *H. murinum*, *H. secalinum* nor *H. silvaticum;* in addition *H. bulbosum*, *H. maritimum* generally gave negative results, infection occurring in only a few cases. The writer has obtained positive results, using the mildew from *H. vulgare*, on *H. distichon*, *H. nudum*, *H. Steudelii* × *trifurcatum*, *H. tetrastichon*, *H. trifurcatum*, *H. vulgare* and *H. Zeocriton*. Young seedlings of *H. nodosum* also proved susceptible, although older plants gave negative results. Negative results were obtained with *H. bulbosum* (except that a few tufts of conidia were produced on one plant), *H. maritimum* and *H. jubatum*. Efforts to transfer this mildew to various grasses, including the other cereals, failed.

Salmon (128) reports the successful infection of *Dactylis glomerata* with conidia from the same host; negative results were obtained with this mildew on *Agropyron repens*, *Lolium temulentum* and the cereals.

Salmon (123, 126, 127) has made extensive tests with the mildew on the brome grasses using conidia from a number of different species. Some of Salmon's more important results are indicated in the following table:

| Source of Conidia | Plants Used as Hosts | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | *Bromus hordeaceus* | *Bromus mollis* | *Bromus interruptus* | *Bromus commutatus* | *Bromus arvensis* | *Bromus tectorum* | *Bromus sterilis* | *Bromus secalinus* | *Bromus velutinus* |
| 1. *Bromus interruptus*..... | 3/3[10] | 48/48 | 10/10 | 0/42 | 0/29 | 16/16 | 0/20 | 0/25 | 11/26[11] |
| 2. *Bromus hordeaceus* var. *glabrescens*..... | | 33/33 | 34/34 | 38/47 | 0/28 | 27/27 | 0/13 | 9/22[11] | 10/16 |
| 3. *Bromus commutatus*.... | | 0/7 | 0/9 | 21/21 | 0/7 | 4/8[11] | 0/7 | 6/7 | 6/7 |
| 4. *Bromus arvensis*..... | | 0/9 | | | 8/8 | | | | |
| 5. *Bromus tectorum*..... | | | | | | 8/8 | 7/8 | | |

From his data, Salmon concluded that four, or possibly even five, specialized races exist within this genus. In looking over his data, however, there seems to be very little, if any, difference between some of them. The races on *B. interruptus* and *B. hordeaceus* differ only in their capacity for infecting *B. commutatus*, the mildew on *B. hordeaceus* infecting this host, while that on *B. interruptus* does not. The race on *B. commutatus* differs from that on *B. hordeaceus* in not infecting *B. mollis* and *B. interruptus*. The race on *B. arvensis* infects this same species but not *B. mollis*. Finally the race on *B. tectorum* differs from that on *B. hordeaceus* in being able to infect *B. sterilis*. It is evident that these races are not distinctly marked off from one another.

But little work has been done using ascospores from various hosts. Marchal (98) mentions the following results: (1) ascospores from *Hordeum vulgare* infected *H. vulgare*, *H. distichon*, *H. trifurcatum* and *H. Zeocriton*, but not *Avena sativa*, *Secale cereale* nor *Triticum vulgare;* (2) ascospores from *Secale cereale* infected *S. cereale*, but not *Hordeum vulgare* nor *Triticum vulgare;* (3) ascospores from *Triticum vulgare* infected *T. vulgare* but not *Agropyron caninum*, *Avena sativa*, *Hordeum vulgare* nor *Secale cereale*. Salmon (124, 132) found that ascospores from *Hordeum vulgare* infected *H. vulgare*, *H. trifurcatum* and *H. Zeocriton*, but not *H. bulbosum*, *H. jubatum*, *H. maritimum*, *H. secalinum*, *Avena sativa*, *Secale cereale* nor *Triticum vulgare;* ascospores from *Bromus commutatus* infected *B. commutatus* and *B. hordeaceus*, but not

[10] The denominator indicates the number of leaves inoculated, the numerator indicates the number infected.

[11] Subinfection.

*B. racemosus.* These results correspond exactly with the infecting capacity of conidia from the same hosts.

The evidence is quite conclusive for the existence of highly specialized races in the grass mildew. For the most part these races are definitely restricted to the species of a single genus of host plants.

**Erysiphe Galeopsidis** DC. Neger (107) tested the infecting capacity of the mildew on *Galeopsis tetrahit* and found that this host was infected, while negative results were obtained on *Calamintha acinos, Glechoma hederacea* and *Stachys recta.* Salmon (128) obtained positive results with the mildew from *Ballota nigra* on this same host but failed to infect *Salvia verticillata* and *Leonurus cardiaca.*

**Erysiphe Polygoni** DC. Neger (107) used the mildew from the following hosts: *Galium silvaticum, Heracleum spondylium, Hypericum perforatum, Ranunculus repens* and *Trifolium incarnatum.* Positive results were obtained when the mildew was sown on plants of the same host from which it was obtained and negative results on all other hosts tested. In one case he noted a slight infection of *Galium silvaticum* with conidia from *Ranunculus repens* but this was probably a foreign infection.

Salmon (123) successfully infected *Pisum arvense* with conidia from *P. sativum.* Other legumes gave negative results. Conidia from *Trifolium pratense* infected this host but gave negative results on seven other species of this genus as well as on species of other genera tested.

**Microsphaera Astragali** (DC.) Trev. The only results recorded for species of this genus are those of Neger (107). He infected *Astragalus glycyphyllus* and *A. cicer* with conidia from the former. Three other hosts gave negative results.

**Uncinula aceris** (DC.) Sacc. and **U. salicis** (DC.) Winter. Neger (107) used conidia of the former species from *Acer pseudoplatanus* to successfully infect *A. pseudoplatanus* and *A. campestre.* Conidia of the second species from *Salix purpurea* infected *S. purpurea* and *S. caprea.*

**Phyllactinia corylea** (Pers.) Karst. Neger (107) reports one test with conidia from *Corylus avellana,* these failing to infect the same host. Voglino (166), using conidia from *Corylus,* infected *Corylus* but not *Carpinus,* and conidia from *Carpinus* infected *Carpinus* but not *Corylus.* He further found that ascospores from *Carpinus* infected *Carpinus* but not *Fagus,* while ascospores from *Fagus* infected *Fagus* but not *Carpinus.*

**Sphaerotheca Humuli** (DC.) Burr. Salmon (128) used conidia of this mildew from *Potentilla reptans* to infect *P. reptans;* no infection occurred on *Agrimonia Eupatoria, Alchemilla arvensis, A. vulgaris, Fragaria* (cult. sp.) *Poterium officinale* nor *Spiraea ulmaria.*

Steiner (150) found that the mildew on *Alchemilla* was confined to the species of this genus. He also claimed to be able to distinguish specialized races within this genus of host plants. He found that conidia from *Alchemilla pastoralis* and *A. flexicaulis* were alike in infecting power except that conidia from the former host would not infect *A. Alpigena* and only slightly *A. pubescens*, while conidia from *A. flexicaulis* infected *A. Alpigena* slightly and *A. pubescens* not at all. Conidia from *A. impexa* would not infect *A. Alpina vera* nor *A. nitida*, while conidia from *A. pastoralis* at least partially infected these hosts. Steiner also found that conidia from the *Vulgares* section of the host genus would not produce full infection on species of the *Alpinae* section, although conidia from species of the latter section vigorously infected species of the former. Steiner noted marked differences in the relation of the species of *Alchemilla* to the mildew, dividing them into the following groups: (1) Susceptible species, as *A. impexa;* (2) immune species, as *A. conjuncta;* (3) species susceptible to the mildew from some hosts, while immune to that from others, as *A. micans.*

**Sphaerotheca Humuli** (DC.) Burr. var. **fuliginea** (Schlecht) Salmon. Salmon (128) has made a few tests with conidia of this mildew from *Plantago lanceolata* and *Taraxacum officinale.* Conidia from the former infected the same host but not *Plantago major* nor *Taraxacum officinale;* conidia from *Taraxacum officinale* infected *T. officinale* but not *Fragaria* (cult. sp.), *Plantago media* nor *P. lanceolata.*

**Oidium** on *Euonymus japonicus.* Salmon (131) reports the following results with this mildew whose identity was not fully determined; conidia from *Euonymus japonicus* infected *E. japonicus* var. *aureus*, var. *albomarginatus*, var. *ovatus aureus*, var. *microphyllus*, var. *President Gunter*, *E. radicans* var. *microphyllus* and var. *Silver Gem*, but not *E. nanus*, *E. americanus* var. *angustifolius*, *E. chinensis*, *E. europaeus*, *E. radicans* var. *carrierei*, *Celastrus scandens*, *C. articulatus*, *C. orixa* nor *Prunus laurocerasus* var. *latifolia.*

## Additional Fungi

Physiological specialization has also been investigated in a few other groups of fungi by a number of different workers, but, outside of the rusts and powdery mildews, no extensive studies have been made.

**Synchytrium taraxaci** de B. and Wor. In the *Chytridiaceae*, Lüdi (95) has tested the infecting capacity of swarmspores of *Synchytrium taraxaci* from *Taraxacum officinale.* He tried to infect nineteen species of Compositae which do not belong to the subdivision Cichoraceae, but with negative results in every case. He also used

twenty-one species which belong to genera of this subgroup, but was able to infect only four species of the genus *Taraxacum*: *T. officinale*, *T. ceratophorum*, *T. palustre* and *T. erythrospermum*. Three other species of this genus tested remained free from the fungus. In many of his experiments, Lüdi kept control plants of *T. officinale* and these were readily infected by the swarmspores.

**Albugo candida** (Pers.) Roussel. Eberhardt (31, 32) has made inoculation tests with this parasite. His results are as follows:

1. Conidia from *Capsella Bursa-pastoris* infected *C. Bursa-pastoris*, *Arabis alpina*, *Iberis amara* and *Lepidium sativum*.
2. Conidia from *Capsella Heegeri* infected *C. Bursa-pastoris* and *Lepidium sativum*.
3. Conidia and oospores from *Lepidium sativum* infected *L. sativum* and *Capsella Bursa-pastoris*.
4. Conidia from *Arabis alpina* infected *A. alpina*, *A. Halleri*, *A. hirsuta*, *A. turrita*, *Capsella Bursa-pastoris*, *Cardamine pratensis*, *Iberis amara*, *Lepidium sativum*, *Senebiera coronopus*, but not *Brassica napus*, *B. nigra*, *B. oleracea*, *Raphanus sativus* nor *Sinapis arvensis*.
5. Conidia from *Brassica Rapa* infected *B. Rapa*, *B. nigra*, *B. oleracea* (var. *botrytis*, *capitata*, *congyloides*), *Diplotaxis tenuifolia* and *Sinapis arvensis*, but not *Capsella Bursa-pastoris*, *Iberis amara* nor *Lepidium sativum*. On the basis of these experiments, Eberhardt concludes that there are two specialized races of the parasite:
    1. On *Arabis-Capsella-Lepidium*.
    2. On *Brassica-Diplotaxis-Sinapis*.

Melhus (99) has also tested the infecting capacity of *Albugo candida* on the radish (*Raphanus sativus*). He was able to infect this host, twenty-two varieties being equally susceptible, also *Raphanus caudatus*, *Brassica alba* (white mustard) and *Brassica oleracea* (cabbage, fifteen varieties). In the case of the latter plants infection was less certain than for the radish. The following plants gave negative results: *Brassica rapa* (turnip, ten varieties), *B. nigra* (black mustard), *B. campestris* (rutabaga, three varieties), *Capsella Bursa-pastoris* (shepherd's purse), *Lepidium sativum* (garden cress), *L. virginicum* (wild pepper grass), *Sisymbrium officinale*, *S. altissimum* (hedge mustard), *Iberis umbellata* (candytuft), *Nasturtium officinale* (water cress) and *Cheiranthus Cheiri* (wall flower).

**Peronospora parasitica** (Pers.) de Bary. Gaumann (59) has carried out a few experiments with this fungus and finds a high degree of host specialization. The fungus that occurs on *Capsella* cannot infect other Cruciferae. The same is true of the race on *Brassica*.

In some cases the parasite seems to be restricted to a single species, for the fungus on *Sisymbrium officinale* does not infect *S. sophia*. On the other hand the same race occurs on *Brassica oleracea* and *B. rapa*.

**Taphrina aurea** (Pers.) Fr. Giesenhagen (60), as a result of his work on the Exoasceae, suggests that *Taphrina aurea*, which infects three species of *Populus*, is becoming specialized into races, each of which is adapted to a single species of *Populus*.

**Claviceps purpurea** (Fr.) Tul. Stäger (142) has found five specialized races in the ergot of rye, *Claviceps purpurea*. One race occurs on rye and also on seventeen other species of grasses; a second race occurs only on *Glyceria fluitans;* a third is confined to species of *Lolium;* a fourth to *Poa annua;* while the fifth is found on *Brachypodium silvaticum* and *Milium effusum*. Both conidia and ascospores, where tested, are limited in the same fashion.

Stäger did not find any such specialization in *Claviceps microcephala*. This ergot is reported on only three grasses.

**Plowrightia morbosa** (Schw.) Sacc. Gilbert (61) reports that *Plowrightia morbosa* (Schw.) Sacc. is specialized on the choke cherry (*Prunus virginiana*) and wild plum (*Prunus americana*). Ascospores, conidia, and pycnospores from the former host were inoculated into the wild plum without giving any evidence of infection. On the other hand, ascospores and conidia under like conditions, readily infected the choke cherry, giving rise to normal knots. A study of the distribution of the fungus on the two hosts lends confirmatory evidence as to the specialization, for in one locality the disease may be prevalent on one host while absent from the other.

**Rhytisma acerinum** (Pers.) Fr. Müller (104) has made a study of this parasite on various maples and concludes that it consists of several specialized races. One race *Platanoides* is found on *Acer platanoides* infecting only slightly *Acer campestris* and *A. pseudoplatanus;* a second race *Campestris* occurs on *Acer campestris*, to a slight extent on *A. platanoides*, but does not occur on *A. pseudoplatanus;* a third race, which is given specific rank as *Rhytisma pseudoplatani*, occurs only on *Acer pseudoplatanus*. Tubeuf (162) inoculated *Acer pseudoplatanus*, *A. platanoides*, *A. campestris* and *A. negundo* with ascospores from the first named host, infection occurring only on this one maple.

**Colletotrichum lindemuthianum** (Sacc. and Magn.) Briosi and Cavara. Barrus (16) has studied the relation of bean varieties to the common anthracnose, *Colletotrichum lindemuthianum*. He tested the susceptibility of one hundred sixty-one varieties to a culture of this organism and found that, while most of the varieties were susceptible in varying degrees, a few seemed to be immune. When, however,

other cultures of the organism were used to inoculate the varieties a different arrangement of susceptibility became evident. Varieties quite immune to the one strain were severely attacked by another strain. All the varieties proved quite susceptible to at least one of the strains used. This indicates the existence of distinct races of this parasite with fairly definite host limitations.

Edgerton and Moreland (33) have made similar studies with cultures of this same fungus. Their results also indicate differences in the infecting capacity of strains of the fungus isolated from different varieties of beans. Some beans, like the snap beans, appear to be quite susceptible to a number of different strains. Other varieties, while quite susceptible to certain strains, are resistant to strains from a different source.

Edgerton and Moreland have also studied cultures of *Glomerella gossypii* (South.) Edg., the cotton anthracnose fungus. They do not find evidence for the existence of specialized strains in this fungus, for all the cultures isolated from different sources were able to infect a large number of cotton varieties.

## General Discussion—Bridging Hosts

The above review of the investigations with reference to host specialization of parasitic fungi indicates that the phenomenon is of general occurrence. The work done is particularly extensive in connection with the rusts and the powdery mildews, but sufficient has been accomplished in other groups to make clear the presence of specialized races.

It is highly probable that the same phenomenon is of wide occurrence among other groups of plant parasites. A large number of so-called species of the Imperfect Fungi, as *Cercospora*, *Phyllosticta*, and *Septoria*, may really be only specialized races of a relatively small number of forms distinct on structural grounds. In several genera of the Imperfect Fungi, as those mentioned, a very large number of species have been recorded; in fact many of them are, mainly at present at least, identified by the host upon which they grow. Cultural experiments may result in grouping many of these together, at the same time making clear the physiological host relations.

We are not, however, to assume that host specialization is of universal occurrence. There are several cases on record where the fungus shows no evidence of the specialization of its hosts. A striking case of this sort is that of *Puccinia subnitens* Diet. Arthur (5) has been able to infect ten hosts, belonging to the families Chenopodiaceae, Cruciferae, and Capparidaceae, with teleutospores from *Distichlis spicata*. Bethel (18), using teleutospores from the same grass, recently

has succeeded in producing aecidia on twenty-two species, belonging to fifteen genera, distributed among six different families, as follows:

1. Polygonaceae: *Polygonum aviculare*, *P. erectum* and *P. ramosissimum*.
2. Chenopodiaceae: *Salsola pestifer*, *Chenopodium album*, *C. glaucum*, *C. lanceolatum*, *C. pagonum*, *Monolepis nuttalliana* and *Kochia scoparia*.
3. Amaranthaceae: *Amaranthus retroflexus* and *A. blitoides*.
4. Nyctaginaceae: *Abronia fragrans*.
5. Cruciferae: *Capsella Bursa-pastoris*, *Lepidium densiflorum*, *L. medium*, *Erysimum asperum*, *Sophia pinnata*, *Roripa palustris*, *Thaspi arvense* and *Sisymbrium altissimum*.
6. Capparidaceae: *Cleome serrulata*.

It is also suggested that species of Papaveraceae may be aecidial hosts for the same rust.

Bock (19) has carried out rather extensive cultural tests with *Puccinia Gentianae* (Str.) Link. He reports no evidence for host specialization, finding that a large number of species of *Gentiana* were readily infected with rust from two different species.

Another illustration of the same condition is reported by Camilla Popta (109) who has been able to infect a number of umbellifers with the same race of *Protomyces macrosporus*. The following plants were infected with the fungus from *Aegopodium podograria*: *Cicuta virosa*, *Seseli montanum*, *Libanotis vulgaris*, *Palimba chalraii*, *Bubon gemmiferum*, *Pachypleurum alpinum*, *Bunium virescens*, *Ferula thyrsiflora*, *Trinia vulgaris* and *Athamanta cretensis*.

If now we compare the degree of specialization found in the different parasitic fungi we find the greatest divergences. In a general way the specialized races may be grouped on the basis of their host range as follows:

1. Specialized races restricted to certain species of a genus of hosts. Here belong the specialized races of *Erysiphe graminis* within the genera *Bromus* and *Hordeum;* of *Puccinia dispersa* within the genus *Bromus;* the specialized races of *Phragmidium disciflorum*, *Puccinia Centaureae*, *P. Epilobii-tetragoni*, *P. Helianthi*, *P. Hieracii*, *P. Pulsatillae*, *P. Ribis*, *P. Ribesii-Caricis*, *P. Caricis-montanae*, *Uromyces Poae*, *U. proeminens* and *Melampsora Euphorbiae*.

2. Specialized races restricted to a particular genus of host plants. A number of specialized races of this sort are known. Among the Erysiphaceae we find the specialized races of *Erysiphe graminis* on *Agropyron*, *Dactylis*, *Poa* and *Secale* and of *Erysiphe cichoracearum* on *Aster* and *Solidago*. Among the rusts we find the races of *Puccinia graminis* on *Aira*, *Poa*, *Calamagrostis* and *Apera;* of *P. coronata* on

*Glyceria*, *Agropyron* and *Bromus;* most of the races of *P. glumarum* and *P. dispersa.*

3. Specialized races occurring on two or more genera but belonging to the same family. As examples, we may mention the specialized races *Avenae*, *Secalis* and *Tritici* of *Puccinia graminis*: *Lolii*, *Calamagrostis* and *Phalaridis* of *P. coronata;* *Secalis* of *P. glumarum;* *Orchidearum-phalaridis* of *P. sessilis;* the races of *P. Ribesii-Caricis*, *P. extensicola*, *P. silvatica*, *P. Bistortae*, *P. mammillata*, *Albugo candida* and *Claviceps purpurea.*

4. Races occurring on hosts belonging to different families as *Puccinia subnitens*, *Uromyces Scirpi* and *Erysiphe cichoracearum.*

When we compare the specialization of a parasite in relation to a particular host we also find the greatest differences. For example *Puccinia graminis avenae* occurs, according to Eriksson (41), on twenty species of grasses belonging to fourteen genera, Carleton (25) recording it on nineteen species belonging to fifteen genera, Jaczewski (68) on seven species belonging to six genera and Stakman and Piemeisel (149) on thirty-three species belonging to twenty-one genera. All agree that this rust occurs on a wide range of more or less unrelated hosts. On the other hand, *Puccinia coronata avenae* is restricted to species of *Avena* and possibly *Arrhenatherum.* The powdery mildew of oats, *Erysiphe graminis avenae*, is also sharply restricted to *Avena*, infecting to some extent *Arrhenatherum.* The crown rust and powdery mildew are similar in infecting a large number of species and varieties of *Avena.*

A similar condition is found in the case of the parasites occurring on *Secale cereale*: *Claviceps purpurea secalis* occurs on eighteen species belonging to eleven genera; *Puccinia graminis secalis*, according to Eriksson (41) on eleven species belonging to five genera and according to Stakman and Piemeisel (149) on twenty-three species belonging to nine genera; *Puccinia glumarum secalis* on *Secale cereale* and *Triticum vulgare;* *Erysiphe graminis secalis* on two species of *Secale;* and *Puccinia dispersa secalis* on *Secale cereale.*

Many of the specialized races, while in the main restricted to certain hosts, yet are able to infect to a greater or less extent a number of other plants. Generally these races are distinguished by their ability to fully infect certain hosts while their development on others is weak and limited. Very good illustrations of such races are found among several of the rusts. The various races of *Coleosporium Campanulae* are not sharply limited to definite hosts, but the hosts of one race may also be attacked by other races. The same is true of the races of *Puccinia graminis*, *P. coronata*, *P. Ribesii-Caricis*, *Melampsora Larici-epitea* and *Uromyces Poae.*

It has repeatedly been suggested by many investigators that specialized races of parasitic fungi may extend their normal host range by passing through certain so-called "bridging hosts." There are many cases known where a particular host plant can be infected by two or more races of a parasite. Such hosts may enable a specialized race to infect a wider range of plants.

Ward (172) apparently was the first to emphasize this possibility as a result of his studies of the behavior of *Puccinia dispersa* on various bromes. Ward supposed that *Bromus arduennensis*, which is readily infected with uredospores of *Puccinia dispersa* from *Bromus mollis* of the section *Serrafalcus*, as well as by uredospores from *B. arduennensis* of the section *Libertia*, served as a means for the rust on bromes of the section *Serrafalcus* to pass over on to bromes of the section *Libertia*. The following data indicate Ward's results as bearing on this point.

| | Uredospores from *Bromus arduennensis* | Uredospores from *Bromus mollis* |
|---|---|---|
| Section *Libertia:* | | |
| *Bromus arduennensis* | 8/7[12] | 13 14 |
| *Bromus arduennensis* var. *villosus* | 10/10 | 1/14 |
| Section *Serrafalcus:* | | |
| *Bromus mollis* | 1/8 | 119/154 |
| *Bromus secalinus* | 8/8 | 31/61 |
| *Stenobromus:* | | |
| *Bromus maximus* | 0/6 | 1/74 |
| *Bromus sterilis* | 0/8 | 4/148 |

An examination of the above data leads one to conclude that the rust on the two hosts, *Bromus arduennensis* and *B. mollis*, are practically identical in their capacity for infecting other bromes. The rust on *Bromus arduennensis* does not have any wider host range than the rust on *B. mollis*. Both grasses appear rather to be hosts for the same strain of rust.

Ward's evidence that *Bromus Krausei* and *B. pendulinus* may serve as bridging hosts is perhaps stronger. The following data indicate the relation of these bromes to the rust on *Bromus sterilis* and *B. mollis*.

| | Uredospores from *Bromus sterilis* | Uredospores from *Bromus mollis* |
|---|---|---|
| *Serrafalcus:* | | |
| *Bromus Krausei* | 14/29[13] | 27/27 |
| *Bromus pendulinus* | 17/65 | 50/50 |
| *Bromus molliformis* | 1/25 | 2/26 |
| *Bromus mollis* | 1/137 | 119/154 |
| *Bromus vestitus* | 1/4 | 3/4 |
| *Stenobromus:* | | |
| *Bromus sterilis* | 126/146 | 4/148 |
| *Bromus gussoni* | 37/60 | 6/53 |

[12] The denominator of the fraction indicates the number of leaves inoculated and the numerator the number infected.

[13] The denominator of the fraction indicates the number of leaves inoculated and the numerator the number infected.

From this data it is evident that *Bromus Krausei* and *B. pendulinus* are susceptible to the rust on both *B. mollis* and *B. sterilis*. From the standpoint of bridging hosts, however, what we need to know is the infecting capacity of uredospores from *B. Krausei* and *B. pendulinus*, produced by inoculation with uredospores from *B. mollis* and *B. sterilis*. It may well be that *B. Krausei* and *B. pendulinus* are merely hosts for the rust on both *B. mollis* and *B. sterilis*. At least the evidence is not complete for proving that they are bridging hosts.

Freeman and Johnson (57) conclude that barley is a bridging host enabling the specialized races of *Puccinia graminis* on wheat and rye to infect oats. They find that the rust on wheat will not infect oats, but will infect barley; the same is true of the rust on rye. When, however, the rust on barley, produced by inoculation from either wheat or rye is sown on oats, infection occurs to a very slight extent. The data upon which this conclusion is based are as follows: (1) uredospores from wheat to barley (26/31),[14] to barley (28/42), to barley (16/16), to oats (2/54); (2) uredospores from rye to barley (23/31), to oats (1/22). As noted before, the barely rust is able to infect all four cereals, but rye and oats less completely than wheat and barley. The indications are that wheat rust and rye rust, as a consequence of growing on barley for one or more generations, are able to infect oats. It is evident, however, that the data obtained are rather meager and very much more extensive series of inoculations should be carried out.

Evans (44) has crossed a wheat (Bob's Rust Proof) resistant to rust (*Puccinia graminis*) with another wheat (Wol Koren) which is highly susceptible. Evans found that the hybrid, although of more vigorous growth than either parent, was much more severely attacked by rust than the susceptible parent. It was also noted that in pot cultures in the greenhouse the hybrid produced an abundance of teleutospores, which rarely occurred on either parent under the same conditions.

Evans next tried to determine the infecting capacities of the rust after it had developed on the hybrid. He found that the rust from the hybrid infected the susceptible parent much more severely than the rust originally found on it. Not only that but the rust on the hybrid readily attacked the resistant parent. Accordingly it is suggested that hybrid plants may play an important part in the transmission of parasites from susceptible to resistant varieties by increasing the virulence of the parasite.

Stakman and Piemeisel (149) record many grasses as hosts for more than one race of *Puccinia graminis*. In fact *Bromus tectorum*,

[14] The denominator of the fraction indicates the number of leaves inoculated and the numerator the number infected.

*Hordeum vulgare*, and *Secale cereale* are infected by all six races that they worked with. They insist, however, that these races are all distinct and that bridging hosts are not present. The grasses which harbor more than one race of rust are, of course, important in the spread of these races, even though they do not enable them to increase their usual host range.

Johnson (69) reports that certain grasses enable the timothy rust to extend its normal range. He found that this rust would not directly infect *Hordeum vulgare* nor *Triticum vulgare*. However, when the timothy rust was transferred to *Avena sativa*, the uredospores produced on this host infected *Hordeum vulgare*. Further uredospores produced on *Festuca elatior* by inoculation from timothy infected both *Hordeum vulgare* and *Triticum vulgare*. It was also found that uredospores from *Dactylis glomerata*, produced by inoculation from timothy, infected *Triticum vulgare*.

Stakman and Jensen (145), however, find no evidence for bridging hosts in the timothy rust. Neither *Avena sativa* nor *Dactylis glomerata* increased the host range. They also report that *Hordeum vulgare* is a host for the timothy rust. Stakman and Piemeisel have further extended the host range of this rust and emphasized its relation to the race *Avenae*.

Arthur (5) suggests that *Helianthus annuus* may be a bridging host for various races of the sunflower rust, *Puccinia Helianthi*, specialized to a narrow range of species of *Helianthus*. *H. annuus* seems to be readily infected by means of teleutospores from other sunflower hosts. Arthur (3, 4) and Kellerman (74, 75) report successful infections with teleutospores from *H. mollis* and *H. grosse-serratus;* Arthur (5) further reports successful infection with teleutospores from *H. laetiflorus* and Kellerman (75) with teleutospores from *H. tuberosus*. The teleutospores from these hosts vary in their ability to infect other *Helianthus* species and, according to results reported, are not able to infect each other except that, according to Arthur, infection of *H. mollis* occurred when teleutospores from *H. laetiflorus* were used.

Neither Arthur nor Kellerman have reported positive tests with the sunflower rust found in nature on *H. annuus* or produced on it experimentally by using spores from other species. Jacky (65) in Europe reports a few tests with teleutospores from *H. annuus;* these were able to infect only three out of eight species tested. As yet no one has clearly shown that the rust on *H. annuus* has a wider range of hosts than the rust on *H. mollis*, *H. grosse-serratus*, etc. In fact, the evidence is much stronger that *H. annuus* is a very susceptible host to the various races of rust occurring on other species of *Helianthus*, if such races really exist, than that *H. annuus* is a bridging host.

In various heteroecious rusts it has been suggested that the aecidial host may act as a bridge for races occurring on the uredo and teleuto hosts to pass over on to other species normally beyond their range of infection. In the case of *Puccinia graminis* the aecidial host, *Berberis vulgaris*, is common to all the races specialized on different kinds of grasses. In the aecidial stage the difference between the races on the gramineous hosts might disappear and the aecidiospores produced on the barberry might have a much wider range of infection.

Several investigators have published data bearing on this point. Eriksson (41) has infected the barberry using teleutospores from more than fifty different grasses. In some of these cases the aecidiospores produced were used to inoculate various gramineous hosts. Some of Eriksson's results may be indicated in the following summary:

| Teleutospores from | Aecidiospores Sown on | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *Avena sativa* | *Bromus arvensis* | *Bromus mollis* | *Dactylis glomerata* | *Koeleria setacea* | *Milium effusum* | *Agropyron repens* | *Bromus secalinus* | *Hordeum vulgare* | *Secale cereale* | *Aira caespitosa* | *Poa compressa* | *Poa pratensis* | *Triticum vulgare* |
| AVENAE | | | | | | | | | | | | | | |
| *Avena sativa* | 2/2[15] | | | 1/1 | | | | | 0/2 | 0/2 | | | | 0/2 |
| *Briza maxima* | 1/1 | | | | | | | | 0/1 | 1/1 | | | | 0/1 |
| *Bromus arvensis* | 1/1 | 0/1 | | | | | | | | | | | | 0/1 |
| *Bromus brachystachys* | 1/1 | 0/1 | | | | | | | 0/1 | 0/1 | | | | 0/1 |
| *Bromus madritensis* | 1/1 | | 1/1 | | | | | | 0/1 | 1/1 | | | | 0/1 |
| *Dactylis glomerata* | 1/1 | | | | | | | | | | | | | |
| *Festuca myurus* | 1/1 | | | | | | | | 0/1 | 1/1 | | | | 0/1 |
| *Festuca tenuiflora* | 1/1 | | | | | | | | 0/1 | 0/1 | | | | 0/1 |
| *Koeleria setacea* | 1/1 | | | | 0/1 | | | | | 0/1 | | | 0/1 | 0/1 |
| *Milium effusum* | 2/2 | | | | | 0/1 | | | | 0/1 | | | | 0/1 |
| *Phalaris canariensis* | 1/1 | | | | | | | | 0/1 | 1/1 | | | | 0/1 |
| *Phleum asperum* | 1/1 | | | | | | | | 0/1 | 0/1 | | | | 0/1 |
| *Vulpia bromoides* | 1/1 | | | | | | | | 0/1 | 0/1 | | | | 0/1 |
| SECALIS | | | | | | | | | | | | | | |
| *Agropyron repens* | 0/1 | | | | | | 1/1 | | 1/1 | 1/1 | | | | 0/1 |
| *Bromus secalinus* | | | | | | | | 0/1 | | 1/1 | | | | |
| *Elymus sibiricus* | | | | | | | | | | 1/1 | | | | |
| *Hordeum vulgare* | 0/2 | | | | | | | | 2/2 | 1/1 | | | | 1/2 |
| *Secale cereale* | 0/2 | | | | | | | | 2/2 | 2/2 | | | | 0/2 |
| AIRAE | | | | | | | | | | | | | | |
| *Aira bottnica* | | | | | | | | | | | 1/1 | | | |
| POAE | | | | | | | | | | | | | | |
| *Poa caesia* | | | | | | | | | | | | 0/1 | 1/1 | |
| *Poa compressa* | 0/1 | | | | | | | | 0/1 | 1/1 | | 1/1 | 0/1 | 0/1 |
| TRITICI | | | | | | | | | | | | | | |
| *Triticum vulgare* | 1/3 | | | | | | | | 2/3 | 1/2 | | | | 6/7 |

In general, the aecidiospores from the barberry are restricted in

[15] The denominator of the fraction indicates the number of tests and the numerator the number that were successful.

their capacity for infection in the same way as uredospores from the same gramineous hosts used as a source of the teleutospores for infecting the barberry. The only marked variation from this is in the case of aecidiospores from the barberry produced by inoculation with teleutospores from *Bromus madritensis*, *Briza maxima*, *Festuca myurus*, and *Phalaris canariensis*, all hosts for the race *Avenae*, which infected not only *Avena sativa* but also *Secale cereale*, a host of race *Secalis* of the rust.

Jaczewski (68) found close correspondence in the infecting capacity of aecidiospores from the barberry arising from teleutospore inoculations from definite plants and that of the uredospores from the same gramineous hosts. In fact his establishment of the nine specialized races of the black stem rust in Russia is based as much on aecidiospore inoculations as on uredospore inoculations.

Stakman (143) also found no essential differences in the infecting capacity of uredospores from wheat and *Agropyron repens* and that of aecidiospores from the barberry arising as a result of inoculation with teleutospores from these same hosts. Pritchard (110) also found a correspondence between the infecting capacity of uredospores and aecidiospores.

Bolley and Pritchard (20) assert that aecidiospores from a single barberry hedge have been used to infect wheat, oats, barley, *Hordeum jubatum*, *Agropyron tenerum* and *A. repens*. The origin of the infection of the barberry was not known but probably was due to teleutospores from *Hordeum jubatum*. In 1905 aecidiospores from barberry readily infected barley and *Hordeum jubatum*, less readily wheat, and oats hardly at all.

Arthur (10), however, has come to the conclusion that the "barberry acts as a bridging host between each and every other gramineous host." The evidence that he gives in support of his statement may be indicated: (1) aecidiospores from barberry, produced by inoculation with teleutospores from *Agrostis alba*, infected wheat and barley, but not oats; (2) aecidiospores from barberry produced by inoculation with teleutospores from *Agropyron tenerum*, infected oats; (3) aecidiospores from the barberry, produced by inoculation with teleutospores from *Sitanion longifolium*, infected wheat; (4) aecidiospores from the barberry, produced by inoculation with teleutospores from *Elymus canadensis*, failed to infect wheat and rye. No one has recorded any data on the infecting capacity of uredospores developed on *Sitanion longifolium;* accordingly we have no information whether this rust is a distinct race or whether *S. longifolium* is merely a host for specialized race *Tritici*. Further, *Agropyron tenerum* is a host for specialized race *Avenae;* hence the results recorded are just what one

would expect. *Agrostis alba*, however, seems to harbor a distinct race of rust and so the result recorded is not in line.

Taking the results of aecidiospore inoculations as a whole, there seems to be no good reason for assuming that aecidiospores from the barberry, produced by teleutospores from a known grass, have any greater range of hosts than uredospores from the same grass. It appears that the racial strains of the black stem rust are not so sharply fixed in their host restrictions in either the uredo or aecidial stage. Further, the nature of the specialization is different in Europe from what it is in America. It is not surprising, then, that these races are able to grow on other hosts. There is, however, no clear indication that the barberry acts in any way as a bridging host and that it enables the races on different grasses to increase their range.

The possibility of the aecidial host serving as a means for extending the host range of specialized races is quite apparent in *Puccinia coronata* Corda. Mühlethaler (102) records *Rhamnus Imeretina* as an aecidial host for specialized races of three of the main subgroups of the crown rust: *Puccinia coronata* (Corda )Kleb., *P. coronifera* Kleb. and *P. alpinae coronata* Mühlethaler. *Rhamnus Purshiana* is likewise an aecidial host for the races on two subgroups—*P. coronata* (Corda) Kleb. and *P. alpinae coronata* Mühlethaler. There is, however, no evidence at hand to indicate that, as a matter of fact, these species do, in any way, act as bridging hosts.

There are many other cases where a particular species of plant is a host for two or more specialized races of a parasite and it might be possible for these to enable the different races to extend their host range. A few cases of this sort may be mentioned. According to Jaczewski (68) *Agropyron repens* and *A. caninum* are hosts for the races *Tritici* and *Secalis* of *Puccinia graminis* and this might serve to enable one race to pass over on to the hosts of the other. There is, however, no experimental proof in support of the suggestion. Stakman and Piemeisel (149) record a number of hosts as common to several or all of the six races they studied. However, no bridging occurs, each race being distinct. According to Mühlethaler (102), *Festuca elatior* is a host for races *Festucae* and *Lolii* of *Puccinia coronata*. *Phalaris arundinacea* is the only uredo and teleuto host for the specialized races of *Puccinia sessilis* with their aecidial stages on Liliaceae, Orchidaceae, Amaryllidaceae and Araceae. Several species of *Ribes* are common aecidial hosts for the specialized races of *Puccinia Ribesii-Caricis*. Similar conditions are found among a large number of other forms—*Uromyces Dactylidis*, *U. Poae*, *U. Fabae*, *U. Scirpi*, *Coleosporium Campanulae*, *Melampsora Larici-epitea*, *M. populina*, *M. Tremulae*, etc.

The occurrence of bridging hosts has been suggested in other groups of parasites as well as in the rusts. Salmon (126, 127), in connection with his work on the powdery mildew of the bromes, has suggested the possibility that *Bromus hordeaceus* may act as a bridging host for the mildew on *Bromus racemosus* and *B. commutatus*. He found that the mildew on *B. racemosus* failed to infect *B. commutatus* (0/12),[16] while it readily infected *B. hordeaceus* (34/34). Furthermore conidia from *B. commutatus* failed to infect *B. racemosus* (0/36), while infecting *B. hordeaceus* (40/49). Salmon supposes that *B. hordeaceus* may act as a bridge for the mildew on *B. racemosus* to pass over to *B. commutatus* and also the reverse. In one case, Salmon infected *B. hordeaceus* with conidia from *B. racemosus*. The conidia produced on the former were then used to infect *B. commutatus*. Salmon, however, did not test the infecting capacity of the conidia thus produced on *B. commutatus*.

Steiner (150), in his work with the mildew (*Sphaerotheca Humuli* (DC.) Burrill) of *Alchemilla*, reports the occurrence of bridging hosts. He states that conidia from *Alchemilla connivens* and *A. pubescens* readily infected *A. pastoralis* and *A. impexa* but gave negative results when sown on *A. micans*. On the other hand, *A. micans* is readily infected with conidia from *A. pastoralis* and *A. impexa*. Accordingly Steiner supposes that *A. pastoralis* and *A. impexa* may carry the mildew over to *A. micans* from *A. connivens* and *A. pubescens*. Some evidence is also given to indicate that *A. impexa* is a bridging host between *A. nitida* and *A. fallax*. Steiner's conclusions, however, are based on only a few tests.

In the Erysiphaceae the question has been raised whether the ascospores and conidia from a particular plant possess the same infecting capacities. Marchal (98), Salmon (124, 132), and Voglino (166) have, in a few cases, used ascospores for inoculation tests and they report that the capacity of ascospores for infection is identical with that of conidia from the same host.

It is, however, somewhat surprising that the evidence that various races of parasites may increase their range by means of bridging hosts is so very meager, if such really occurs. In those cases where the suggestion of bridging has been most emphasized one is not impressed with the data supplied. In fact, in all such cases the races of the parasite are not sharply limited in their host range. They may infect some hosts more readily and more vigorously than others, but the virulence of the parasite does not seem to be increased or decreased by developing on congenial or uncongenial hosts.

[16] The denominator of the fraction indicates the number of leaves inoculated and the numerator the number infected.

The notion of bridging hosts, of course, implies that the fungus undergoes a physiological change in consequence of its new habitat and thus becomes able to attack other hosts. The change is certainly closely associated with variation in virulence so well known in the case of pathogenic bacteria. It is quite likely that fungous parasites vary in virulence or can be made to do so by suitable experimental methods. At present, however, we have no good evidence that this has been done in any particular case. The results of Evans (44), referred to above, point in this direction. In this case, however, the data are not at all extensive. The facts might be explained by an increase in susceptibility of both resistant and susceptible parent in response to a change in the environment; or external factors may have favored a more successful invasion on the part of the rust parasite. Passing reference may be made to the work of Salmon (129, 130), Ward (173), Stakman (143) and Spinks (141) which clearly indicates that a plant may be rendered more or less susceptible to fungous invasion by means of certain agencies. The work of these investigators shows that mineral starvation, excess of nutrients, mechanical injuries, anaesthetics, etc., modify the relations of a plant to fungous invasion.

It has been pointed out by Eriksson (35), Ward (172, 174), Vavilov (164, 165) and others that a specialized race tends to occur on more or less closely related hosts. There are, however, great differences among the specialized races in this respect. As pointed out above, the host range of these races may be narrow or wide. Within a single species of parasite we may have a race occurring on many hosts belonging to different genera and another race restricted to a single genus or even certain species of a genus. *Puccinia graminis*, as well as other fungi, includes races of such wide differences in host range.

Attempts have been made to utilize the infective capacity of a parasite to determine the genetic relationship of hosts. Eriksson (35) applied this test in determining the possible relation of a rye-wheat hybrid to the two parents. Ward (171, 172) reports a fairly close correspondence between the hosts of the more or less well-defined races of *Puccinia dispersa bromi* and the grouping of the bromes on other grounds. Vavilov (154, 155) has used *Puccinia dispersa tritici* and *Erysiphe graminis tritici* as a test in determining the relationship of types and varieties of *Triticum*. He also used *Puccinia graminis avenae* and *P. coronata avenae* as a similar test in connection with species and varieties of *Avena*. It is interesting to note that the parasites on wheat gave practically the same results and these are both quite narrowly specialized races. The rusts on oats, however, did not give corresponding results, *Puccinia graminis avenae* infecting a wider

range of varieties than *P. coronata avenae*. The former, as noted above, occurs on a number of species of grasses belonging to different genera, whereas the latter is closely restricted to the genera *Avena* and *Arrhenatherum*.

It has been suggested that there is a connection between stability of host species and the occurrence of specialized races. Edgerton and Moreland (33) suppose that the explanation of the difference between Bean Anthracnose and Cotton Anthracnose is due to the fact that bean varieties are quite distinct and well marked, with little or no crossing and, accordingly, no intergrading forms. On the other hand, cotton varieties readily cross and thus a series of intergrading forms occurs onto which the anthracnose fungus may spread. This explanation, however, cannot have any very general explanation. The evidence indicates that the willows hybridize quite readily and yet a number of specialized races of willow rusts are recorded.

Magnus (96) suggested that the existence of these specialized races may indicate an adaptation on the part of the parasite to live on particular hosts. He makes a distinction between adaptive races and biologic forms. The former term is applied to strains or races of a parasite which tend to infect certain hosts more readily than others. On the other hand, the biologic form is sharply restricted to its hosts. Dietel (30) points out that a parasite may first have attacked a wide range of hosts, gradually becoming broken up into races adapted to certain hosts and finally limited to them. It is possible that the relative abundance of the hosts may have been a factor in this process. The presence or absence of hosts in a given locality may also have played a part.

The question has often been raised as to whether these specialized races of fungi are constant or fixed. Montemartini (100) has recently raised the question again as a result of his studies with certain parasites. He inclines to believe that these races are not fixed and definite and so capable of being carried from one region to another but rather that they are local adaptive forms, perhaps dependent on the variability or distribution of the host plants. He suggests that they are not permanent but temporary, owing their origin to the various nutritive conditions afforded by different hosts.

I have already called attention to the fact that some specialized races are distinguished by their ability to infect some hosts more fully than others. The races of *Puccinia Ribesii-Caricis*, *P. Hieracii*, *P. graminis*, *Uromyces Dactylidis* and *Coleosporium Campanulae* afford illustrations of this condition. The infection or non-infection of certain hosts is dependent to a great extent upon particularly favorable experimental conditions. It is well known that various factors do

influence in a striking way the capacity of a parasite for infecting hosts.

The extent of the stability of specialized races must vary greatly in different cases. Some of the forms above considered are doubtless as fixed and constant as many parasites which show structural differences. Mention may be made of the races of *Melampsora Tremulae* as illustrating a good case of *physiological species*. In studying the races of *Erysiphe graminis* one also gets a strong impression of their constancy and definiteness and they seem as real as though separable by structural features.

In other cases, however, this is not true. One is not impressed with the definiteness of races in *Puccinia Helianthi*, *P. Hieracii* and others. These are not characterized by well-defined host limitations. Perhaps one is justified in distinguishing different types of specialization as physiological species, races, strains, etc.

But little data are available for comparing the specialization of the same fungus in widely separated localities. The specialization of *Puccinia graminis* is apparently the same in Sweden and Russia but it has taken a quite different course in North America. Treboux (159, 160) finds a different condition in *Puccinia coronata* in southern Russia from what Eriksson (37, 42) finds in Sweden and Mühlethaler (102) finds in Switzerland. Carleton's (26) results in the United States also diverge widely from those of Eriksson. Arthur (11, 13) does not find evidence for specialization in *Puccinia Ribesii-Caricis* in this country, while Klebahn (87, 91) reports several fairly well-defined races of this rust in Europe. On the other hand, there seems to be no essential difference in the specialization of *Erysiphe graminis* in Europe and North America. The same sharp host limitation seems to occur in both countries. Further data are necessary before we are able to determine the relation between the specialization of parasites in different regions.

In a few cases the races are also characterized by minor structural differences. Freeman and Johnson (57) and later Stakman and Piemeisel (149) have noted variations in the size and shape of the uredospores which distinguish the races of *Puccinia graminis*. Klebahn (87, 91) has noted similar differences in the spores of the various races of *Puccinia Absinthi*, *Melampsora Larici-epitea* and others.

Fischer (46, 47), as well as others, has suggested that physiological specialization is a starting point for the origination of forms distinct on structural grounds. The suggestion is plausible, for it is possible to arrange a series of forms ranging from races differing in host relations through all stages to others showing constant structural differences.

The general occurrence of specialized races of parasitic fungi makes their study particularly important. It is especially desirable to know the exact host relations of the different races as well as to determine whether the races are stable and constant or whether they are capable of a change of virulence and consequently able to extend their host range.

## LITERATURE CITED


1. **Arthur, J. C.** Cultures of Uredineae in 1899. Bot. Gaz. **29**: 268–276. 1900.
2. —— Cultures of Uredineae in 1900 and 1901. Journ. Mycol. **8**: 51–56. 1902.
3. —— Cultures of Uredineae in 1902. Bot. Gaz. **35**: 10–23. 1903.
4. —— Cultures of Uredineae in 1903. Journ. Mycol. **10**: 8–21. 1904.
5. —— Cultures of Uredineae in 1904. Journ. Mycol. **11**: 50–67. 1905.
6. —— Cultures of Uredineae in 1905. Journ. Mycol. **12**: 11–27. 1906.
7. —— Cultures of Uredineae in 1906. Journ. Mycol. **13**: 189–205. 1907.
8. —— Cultures of Uredineae in 1907. Journ. Mycol. **14**: 7–26. 1908.
9. —— Cultures of Uredineae in 1908. Mycologia **1**: 225–256. 1909.
10. —— Cultures of Uredineae in 1909. Mycologia **2**: 213–240. 1910.
11. —— Cultures of Uredineae in 1910. Mycologia **4**: 7–33. 1912.
12. —— Uredinales. North American Flora **7** (Part 3): 161–268. 1912.
13. —— Cultures of Uredineae in 1912, 1913 and 1914. Mycologia, **7**: 61–89. 1915.
14. —— Cultures of Uredineae in 1915. Mycologia **8**: 125–141. 1916.
15. **Bandi, W.** Beiträge zur Biologie der Uredineen (Phragmidium subcorticium, Puccinia Caricis montanae). Hedwigia **42**: 118–152. 1903.
16. **Barrus, M. F.** Variation of Varieties of Beans in their Susceptibility to Anthracnose. Phytopathology **1**: 190–195. 1911.
17. **de Bary, A.** Neue Untersuchungen über Uredineen. Zweite Mitteilung. Monatsberichten der Akademie der Wissenschaften zu Berlin (1866): 205–215.
18. **Bethel, E.** Puccinia subnitens and its Aecial Hosts. Phytopathology **7**: 92–94. 1917.
19. **Bock, R.** Beiträge zur Biologie der Uredineen. Centralbl. f. Bakt. Abt. II, **20**: 564–592. 1908.
20. **Bolley, H. L. and Pritchard, F. J.** Rust Problems. Facts, Observations and Theories; Possible Means of Control. N. Dak. Agr. Exp. Stat. Bull. **68**: 607–676. 1906.
21. **Bubák, Fr.** Über einige Umbelliferen bewohnende Puccinien. 1. Sitzungsber. Königl. böhmischen Gesell. d. Wissenschaften in Prag (1900): Nr. 26: 1–8.
22. —— Ueber die Puccinien vom Typus der Puccinia Anemones—virginianae Schweinitz. Sitzungsber. d. Königl. böhmischen Gesell. der Wissenschaften in Prag, Math. naturwissen. Klasse. No. 2: 1–11. 1901.
23. —— Einige neue oder kritische Uromyces-Arten. Sitzungsber. d. Königl. böhmischen Gesell. der Wissenschaften in Prag (1902): 1–23.
24. —— Infektionsversuche mit einigen Uredineen. II. Bericht (1903). Centralbl. f. Bakt. Abt. II, **12**: 411–426. 1904.
25. **Carleton, M. A.** Cereal Rusts of the United States. U. S. Dept. Agr. Div. Veg. Physiol. and Path. Bull. **16**: 74 pp. 1899.
26. —— Investigations of Rusts. Bur. Pl. Ind. Bull. **63**: 32 pp. 1904.

27. **Dietel, P.** Über die Aecidien von Melampsora Euphorbiae dulcis Otth und Puccinia silvatica Schroet. Oesterreichische bot. Zeitschr. **39**: 256–259. 1889.
28. —— Über den Generationswechsel von Uromyces lineolatus (Desm.) Schroet. Hedwigia **29**: 149–152. 1890.
29. —— Über Rostpilze mit wiederholter Aecidienbildung. Flora, **81**: 394–404. 1895.
30. —— Waren die Rostpilze in frühern Zeiten plurivor? Bot. Centralbl. **79**: 81–85, 113–117. 1899.
31. **Eberhardt, A.** Zur Biologie von Cystopus candidus. Centralbl. f. Bakt. Abt. II, **10**: 655–656. 1904.
32. —— Contribution á l'étude de Cystopus candidus. Centralbl. f. Bakt. Abt. II. **12**: 235–249; 426–439; 614–631; 714–727. 1904.
33. **Edgerton, C. W. and Moreland, C. C.** Experiments on Varietal Resistance to the Bean and Cotton Anthracnose Diseases. La. Agr. Exp. Sta. Bull. 155. 24 pp. 1916.
34. **Eriksson, J.** Über die Specialisirung des Parasitismus bei den Getreiderostpilzen. Ber. d. d. bot. Gesell. **12**: 292–331. 1894.
35. —— Ein parasitischer Pils als Index der inneren natur eines Pflanzenbastards. Bot. Notiser (1895): 251–253.
36. —— Neue Untersuchungen über die Specialisirung, Verbeitung und Herkunft des Schwarzrostes (Puccinia graminis Pers.). Jahr. f. wissen. Bot. **29**: 499–524. 1896.
37. —— Neue Beobachtungen über die Natur und das Vorkommen des Kronenrostes. Centralbl. f. Bakt. Abt. II, **3**: 291–308. 1897.
38. —— A General Review of the Principal Results of Swedish Research into Grain Rust. Bot. Gaz. **25**: 26–38. 1898.
39. —— Étude sur le Puccinia Ribis DC. des Groseillers rouges. Rev. générale de Botanique **10**: 497–506. 1898.
40. —— Nouvelles études sur la rouille brune des céreales. Ann. Sci. Nat. (Ser. 8) **9**: 241–288. 1899.
41. —— Über die Specizialisierung des Getreideschwarzrostes in Schweden und in anderen Ländem. Centralbl. f. Bakt. Abt. II, **9**: 590–607, 654–658. 1902.
42. —— Neue Studien über die Spezialisierung der grasbewohnenden Kronenrostarten. Arkiv. för Botanik, 8 (No. 3). 26 pp. 1908.
43. **Eriksson, J. and Henning, E.** Die Getreideroste, ihre Geschichte und Natur, sowie Massregeln gegen dieselben. 1896.
44. **Evans, J. B. P.** South African Cereal Rusts, with Observations on the Problem of Breeding Rust-resistant Wheats. Journ. Agr. Sci. **4**: 95–104. 1911.
45. **Fischer, Ed.** Die Uredineen der Schweiz. Beiträge zur Kryptogamenflora der Schweiz. 2 (Heft II). 1904.
46. —— Die biologischen Arten der parasitischen Pilze und die Entstehung neuer Formen im Pflanzenreich. Atti della Societa elvetica di Scienze naturali adunata in Locarno. 86 Sessione: 49–62. 1904.
47. —— Der Speciesbegriff bei den parasitischen Pilzen. Verhandl. der Schweizer. Naturforschenden Gesellsch. 88 Jahresversammlung. pp. 300–308. 1905.
48. —— Beiträge zur Entwicklungsgeschichte der Uredineen. Centralbl. f. Bakt. Abt. II. **28**: 139–143. 1910.
49. —— Über die Specialisation des Uromyces caryophyllinus (Schrank) Winter. (Vorläufige Mitteilung.) Mycol. Centralbl. **1**: 1, 2. 1912.
50. —— Beiträge zur Biologie der Uredineen. 3. Die Specialisation des Uromyces caryophyllinus (Schrank) Winter. Mycol. Centralbl. **1**: 307–313. 1912.

51. —— Beiträge zur Biologie der Uredineen. 4. Weitere Versuche über die Specilisation des Uromyces caryophyllinus (Schrank) Winter. Mycol. Centralbl. 3: 145–149. 1913.
52. —— Beiträge zur Biologie der Uredineen. 5. Puccinia Pulsatillae Kalchbr. (Syn. Puccinia de Baryana Thüm) und Theoretisches über die Specialisation. Mycol. Centralbl. 3: 214–220. 1913.
53. —— Mykologische Beiträge. 1. Die Wirtswahl bei der Alchimillenbewohnenden Uromyces. Mitteilungen d. Naturforschenden Gesellschaft in Bern (1915): 214–234. 1916.
54. —— Mykologische Beiträge. 11. Mitteilungen d. Naturforschenden Gesellschaft in Bern (1916). 1917.
55. **Fraser, W. P.** Cultures of Heteroecious Rusts. Mycologia 4: 175–193. 1912.
56. **Freeman, E. M.** Experiments on the Brown Rust of Bromes (Puccinia dispersa). Ann. Bot. 16: 487–494. 1902.
57. **Freeman, E. M. and Johnson, E. C.** The Rusts of Grains in the United States. Bur. Pl. Ind. Bull. 216. 87 pp. 1911.
58. **Gassner, Gustav.** Die Getreideroste und ihr Auftreten im subtropischen östlichen Südamerika. Centralbl. f. Bakt., Abt. II, 44: 305–381. 1915.
59. **Gaumann, E.** Centralbl. f. Bakt. Abt. II, 45: 575–577. 1916.
60. **Giesenhagen, K.** Die Entwickelungsreihen der parasitischen Exoasceen. Flora 81: 267–361. 1895.
61. **Gilbert, E. M.** Biologic Forms of Black Knot. Phytopathology 3: 246, 247. 1913.
62. **Hasler, A.** Beiträge zur Kenntnis der Crepis- und Centaurea-Puccinien vom Typus der Puccinia Hieracii. Centralbl. f. Bakt. Abt. II, 21: 510–511. 1908.
63. **Hitchcock, A. S. and Carleton, M. A.** Second Report on Rusts of Grain. Kans. Agr. Exp. Sta. Bull. 46. 9 pp. 1894.
64. **Jacky, E.** Die Compositen-bewohnenden Puccinien vom Typus der Puccinia Hieracii und der Spezialisierung. Zeitschr. f. Pflanzenkr. 9: 193–224, 263–295, 330–346. 1899.
65. —— Beitrag zur Kenntnis der Rostpilze. Centralbl. f. Bakt. Abt. II, 9: 746–804, 841–844. 1902.
66. **Jacob, Gina.** Zur Biologie Geranium bewohnender Uredineen. (Vorläufige Mitteilung.) Mycol. Centralbl. 3: 158, 159. 1913.
67. —— Zur Biologie Geranium bewohnender Uredineen. Centralbl. f. Bakt. Abt. II, 44: 617–658. 1915.
68. **Jaczewski, A. von.** Studien über das Verhalten des Schwarzrostes des Getreides in Russland. Zeitsch. f. Pflanzenkr. 20: 321–359. 1910.
69. **Johnson, E. C.** Timothy Rust in the United States. Bur. Pl. Ind. Bull. 224. 20 pp. 1911.
70. **Jordi, E.** Culturversuche mit Papilionaceen-bewohnenden Rostpilzen. (Vorläufige Mitteilung.) Centralbl. f. Bakt. Abt. II, 10: 777–779. 1903.
71. —— Beiträge zur Kenntniss der Papilionaceen-bewohnenden Uromycesarten. Centralbl. f. Bakt. Abt. II, 11: 763–795. 1904.
72. **Juel, H. O.** Mykologische Beiträge V. Öfversigt af k. Vetenskaps-Akad. Förhandlinger, 53: 213–224. 1896.
73. —— Ein Beitrag zur Kenntnis des Uromyces Poae Rabenh. Svensk Botanisk Tidskrift 2: 169–174. 1908.
74. **Kellerman, W. A.** Uredineous Infection Experiments in 1903. Journ. Mycol. 9: 225–238. 1903.

75. —— Uredineous Infection Experiments in 1904. Journ. Mycol. **11**: 26–33. 1905.
76. **Klebahn, H.** Kulturversuche mit heteroecishen Uredineen. Zeitschr. f. Pflanzenkr. **2**: 258–275, 332–343. 1892.
77. —— Kulturversuche mit heteroecishen Uredineen. II. Bericht (1893). Zeitschr. f. Pflanzenkr. **4**: 7–13, 85–90, 129–139. 1894.
78. —— Kulturversuche mit heteroecishen Rostpilzen. III. Bericht (1894). Zeitschr. f. Pflanzenkr. **5**: 13–18, 69–79, 149–156. 1895.
79. —— Kulturversuche mit heteroecishen Rostpilzen. IV. Bericht (1895). Zeitschr. f. Pflanzenkr. **5**: 257–268, 327–333. 1895.
80. —— Kulturversuche mit heteroecischen Rostpilzen. V. Bericht (1896). Zeitschr. f. Pflanzenkr. **6**: 257–270, 324–338. 1896.
81. —— Kulturversuche mit heteroecischen Rostpilzen. VI. Bericht (1897). Zeitschr. f. Pflanzenkr. **7**: 325–345, **8**: 11–30. 1897–98.
82. —— Kulturversuche mit heteroecischen Rostpilzen. VII. Bericht (1898). Zeitschr. f. Pflanzenkr. **9**: 14–26, 88–99, 137–160. 1899.
83. —— Kulturversuche mit Rostpilzen. VIII. Bericht (1899). Jahr. f. wissen. Bot. **34**: 347–404. 1900.
84. —— Kulturversuche mit Rostpilzen. IX. Bericht (1900). Jahr. f. wissen. Bot. **35**: 660–710. 1901.
85. —— Kulturversuche mit Rostpilzen. X. Bericht (1901). Zeitschr. f. Pflanzenkr. **12**: 17–44, 132–151. 1902.
86. —— Kulturversuche mit Rostpilzen. XI. Bericht (1902). Jahrbuch d. Hamburgischen wissenschaftlichen Anstalten **20**: 1–56. 1903.
87. —— Die wirtswechselnden Rostpilze. 1904.
88. —— Kulturversuche mit Rostpilzen. XII. Bericht (1903 und 1904). Zeitschr. f. Pflanzenkr. **15**: 65–108. 1905.
89. —— Kulturversuche mit Rostpilzen. XIII. Bericht (1905 und 1906). Zeitschr. f. Pflanzenkr. **17**: 129–157. 1907.
90. —— Kulturversuche mit Rostpilzen. XIV. Bericht (1907–1911). Zeitschr. f. Pflanzenkr. **22**: 321–350. 1912.
91. —— Uredineen. Kryptogamenflora der Mark Brandenburg **5a**: 69–904. 1914.
92. —— Aufgaben und Ergebnisse biologischer Pilzforschung. Vorträge aus dem Gesamtgebiet der Botanik, Heft I. 41 pp. 1914.
93. **Krieg, W.** Experimentelle Untersuchungen über Ranunculus-Arten bewohnende Uromyces. Centralbl. f. Bakt. Abt. II, **19**: 697–714, 771–788. 1907.
94. —— Neue Infektionsversuche mit Uromyces Dactylidis. Centralbl. f. Bakt. Abt. II, **25**: 430–436. 1909.
95. **Lüdi, R.** Beiträge zur Kenntniss der Chytridiaceen. Hedwigia **40**: 1–44. 1901.
96. **Magnus, P.** Die systematische Unterscheidung nächst verwandter parasitischer Pilze auf Grund ihres verschieden biologischen Verhaltens. Hedwigia **33**: 362–366. 1894.
97. **Marchal, E.** De la specialisation du parasitisme chez l'Erysiphe graminis. Compt. Rend. **135**: 210–212. 1902.
98. —— De la specialisation du parasitisme chez l'Erysiphe graminis. Compt. Rend. **136**: 1280, 1281. 1903.
99. **Melhus, I. E.** Experiments on Spore Germination and Infection in Certain Species of Oomycetes. Wis. Agr. Exp. Sta. Res. Bull. **15**: 25–91. 1911.
100. **Montemartini, L.** Sopra la specializzazione dei funghi parassiti, con particolare riguardo alla specializzazione delle ruggini dei cereali. Rivista di Patalogia Vegetale, year 8: 33–44, 145–158. 1916.

101. **Mühlethaler, F.** Infektionsversuche mit Kronenrosten. Centralbl. f. Bakt. Abt. II, **26**: 58. 1910.
102. —— Infektionsversuche mit Rhamnus befallenden Kronenrosten. Centralbl. f. Bakt. Abt. II, **30**: 386–419. 1911.
103. **Müller, F.** Beiträge zur Kenntniss der Grasroste. Beihefte zum Bot. Centralbl. **10**: 181–212. 1901.
104. **Müller, K.** Zur Biologie der Schwarzfleckenkrankheit der Ahornbäume, hervorgerufen durch den Pilz Rhytisma acerinum. Centralbl. f. Bakt. Abt. II, **36**: 67–98. 1912.
105. **Müller, W.** Versuche mit Uredineen auf Euphorbien und Hypericum. Centralbl. f. Bakt. Abt. II, **17**: 210, 211. 1906.
106. —— Zur Kenntnis der Euphorbia-bewohnenden Melampsoren. Centralbl. f. Bakt. Abt. II, **19**: 441–460, 544–563. 1907.
107. **Neger, F. W.** Beiträge zur Biologie der Erysipheen. Flora **90**: 221–272. 1902.
108. **Plowright, C. B.** A Monograph of the British Uredineae and Ustilagineae. 1889.
109. **Popta, Miss C. M. L.** Beiträge zur Kenntnis der Hemiasci. Flora **86**: 1–46. 1899.
110. **Pritchard, F. J.** A Preliminary Report on the Yearly Origin and Dissemination of Puccinia graminis. Bot. Gaz. **52**: 169–192. 1911.
111. **Probst, R.** Versuche mit Kompositen-bewohnenden Puccinien. (Vorläufige Mitteilung.) Centralbl. f. Bakt. Abt. II, **19**: 543, 544. 1907.
112. —— Infektionsversuche mit Kompositen-bewohnenden Puccinien. Annales Mycol. **6**: 289–300. 1908.
113. —— Die Spezialisation der Puccinia Hieracii. Centralbl. f. Bakt. Abt. II, **22**: 676–720. 1909.
114. **Reed, George M.** Infection Experiments with Erysiphe graminis DC. Trans. Wis. Acad. Sciences, Arts and Letters **15**: 135–162. 1906.
115. —— Infection Experiments with the Mildew on Cucurbits, Erysiphe cichoracearum DC. Trans. Wis. Acad. Sciences, Arts, and Letters **15**: 527–547. 1907.
116. —— Infection Experiments with Erysiphe cichoracearum DC. Bull. Univ. Wisc. (Science Series) **3**: 337–416. 1908.
117. —— The Mildews of the Cereals. Bull. Torrey Bot. Club **36**: 353–398. 1909.
118. —— Infection Experiments with the Powdery Mildew of Wheat. Phytopathology **2**: 81–87. 1912.
119. —— The Powdery Mildews—Erysiphaceae. Trans. Amer. Micro. Soc. **32**: 219–258. 1913.
120. —— The Powdery Mildews of Avena and Triticum. Mo. Agr. Exp. Sta. Res. Bull. 23. 19 pp. 1916.
121. **Rostrup, E.** Mykologiske Meddelelser, IV. Botanisk Tidsskrift **18**: 36–47. 1894.
122. —— Biologiske Arter og Racer. Botanisk Tidsskrift **20**: 116–125. 1896.
123. **Salmon, E. S.** On Specialization of Parasitism in the Erysiphaceae. Beihefte zum Bot. Centralbl. **14**: 261–315. 1903.
124. —— Infection Powers of Ascospores in Erysiphaceae. Journ. of Botany **41**: 159–165, 204–212. 1903.
125. —— Cultural Experiments with the Barley Mildew, Erysiphe graminis DC. Annales Mycol. **2**: 70–99. 1904.

126. —— On Erysiphe graminis DC. and its Adaptive Parasitism within the Genus Bromus. Annales Mycol. **2**: 255–267, 307–343. 1904.
127. —— Recent Researches on the Specialization of Parasitism in the Erysiphaceae. The New Phytologist **3**: 55–60. 1904.
128. —— On Specialization of Parasitism in the Erysiphaceae, II. The New Phytologist **3**: 109–121. 1904.
129. —— Cultural Experiments with "Biologic Forms" of the Erysiphaceae. Phil. Trans. Royal Society of London B. **197**: 107–122. 1904.
130. —— Further Cultural Experiments with "Biologic Forms" of the Erysiphaceae. Ann. Bot. **19**: 125–148. 1905.
131. —— Cultural Experiments with an Oidium on Euonymus japonicus Linn. Annales Mycol. **3**: 1–15. 1905.
132. —— On Specialization of Parasitism in the Erysiphaceae, III. Annales Mycol. **3**: 172–184. 1905.
133. **Schneider, O.** Versuche mit schweizerischen Weidenmelampsoren. Centralbl. f. Bakt. Abt. II, **13**: 222–224. 1904.
134. —— Weitere Versuche mit schweizerischen Weidenmelampsoren. Centralbl. f. Bakt. Abt. II, **15**: 232–234. 1905.
135. —— Experimentelle Untersuchungen über schweizerische Weidenrostpilze. Centralbl. f. Bakt. Abt. II, **16**: 74–93, 159–176, 192. 1906.
136. **Schroeter, J.** Entwicklungsgeschichte einiger Rostpilze II, III. Cohn's Beiträge zur Biologie der Pflanzen **3**: 51–93. 1879.
137. —— Die Pilze Schlesien Uredinei. Kryptogamen-Flora v. Schlesien. **3**: 291–381. 1889.
138. —— Zur Entwicklungsgeschichte der Uredineen. Jahrsber. d. Schles. Ges. f. vaterl. Cult. (Bot. Sect.) **71**: 31, 32. 1893.
139. **Semadeni, O.** Kulturversuche mit Umbelliferen bewohnenden Rostpilzen. Centralbl. f. Bakt. Abt. II, **10**: 522–524. 1903.
140. —— Beiträge zur Kenntnis der Umbelliferen bewohnenden Puccinien. Centralbl. f. Bakt. Abt. II, **13**: 73–81, 214–221, 338–352, 439–448, 527–543. 1904.
141. **Spinks, G. T.** Factors Affecting Susceptibility to Disease in Plants. Journ. Agr. Science **5**: 231–247. 1913.
142. **Stäger, R.** Infektionsversuche mit Gramineen-bewohnenden Clavicepsarten. Bot. Zeitung **61**: 111–158. 1903.
143. **Stakman, E. C.** A Study in Cereal Rusts, Physiological Races. Minn. Agr. Exp. Sta. Bull. 138, 56 pp. 1914.
144. —— A Preliminary Report on the Relation of Grass Rusts to the Cereal Rust Problem. Phytopathology **4**: 411. 1914.
145. **Stakman, E. C. and Jensen, Louise.** Infection Experiments with Timothy Rust. Journ. Agr. Res. **5**: 211–216. 1915.
146. **Stakman, E. C. and Piemeisel, F. J.** Infection of Timothy by Puccinia graminis. Journ. Agr. Res. **6**: 813–816. 1916.
147. —— Biologic Forms of Puccinia graminis on Wild Grasses and Cereals. Phytopathology **6**: 99, 100. 1916.
148. —— A New Strain of Puccinia graminis. Phytopathology **7**: 73. 1917.
149. —— Biologic Forms of Puccinia graminis on Cereals and Grasses. Journ. Agr. Res. **10**: 429–502. 1917.
150. **Steiner, J. A.** Die Specialization der Alchemillenbewohnenden Sphaerotheca Humuli (DC.) Burr. Centralbl. f. Bakt. Abt. II, **21**: 677–726. 1908.
151. **Sydow, P. and H.** Monographia Uredinearum. 3 Volumes. 1904–1915.
152. **Tranzschel, W.** Versuche mit heteroecischen Rostpilzen (Vorläufige Mitteilung). Centralbl. f. Bakt. Abt. II, **11**: 106. 1903.

153. —— Neue Fälle von Heteröcie bei den Uredineen. Trav. du Mus. Bot. de l'Acad. Impér. d. Sci. St. Pétersbourg 2: 14–30. 1904.
154. —— Beiträge zur Biologie der Uredineen. Bericht über die im Jahre 1904 ausgeführten Kulturversuche. Trav. du Mus. Bot. de l'Acad. Impér. d. Sci. St. Pétersbourg 2: 64–80. 1904.
155. —— Beiträge zur Biologie der Uredineen. III. Trav. du Mus. Bot. d. l'Acad. Impér. d. Sci. St. Pétersbourg 7: 1–19. 1909.
156. —— Ueber einige Aecidien mit gelbbrauner Sporenmembran. Trav. du Mus. Bot. d. l'Acad. Impér. d. Sci. St. Pétersbourg 7: 111–116. 1910.
157. —— Die auf der Gattung Euphorbia auftretenden autöcischen Uromyces-Arten. Annales Mycol. 8: 1–35. 1910.
158. —— Culturversuche mit Uredineen in den Jahren 1911–1913. (Vorläufige Mitteilung.) Mycol. Centralbl. 4: 70, 71. 1914.
159. **Treboux, O.** Infektionsversuche mit parasitischen Pilzen, III. Annales Mycol. 10: 557–563. 1912.
160. —— Infektionsversuche mit parasitischen Pilzen, IV. Annales Mycol. 12: 480–483. 1914.
161. —— Überwinterung vermittels Mycels bei einigen parasitischen Pilzen. Mycol. Centralbl. 5: 120–126. 1914.
162. **Tubeuf, F. K. von.** Infektionsversuche mit Uredineen der Weisstanne. Centralbl. f. Bakt. Abt. II, 9: 241. 1902.
163. —— Rassenbildung bei Ahorn-Rhytisma. Naturwiss. Zeitschr. Forst.- und Landwirtschr. 11: 21–24. 1913.
164. **Vavilov, N. I.** Beiträge zur Frage über die verschiedene Widerstandsfähigkeit der Getreide gegen parasitische Pilze. Arbeiten d. Versuchsstation für Pflanzenzüchtung am Moskauer landwirtsch. Institut, 1 Folge, 1–110. 1913.
165. —— Immunity to Fungous Diseases as a Physiological Test in Genetics and Systematics, Exemplified in Cereals. Jour. of Genetics, 4: 49–65. 1914.
166. **Voglino, P.** Contribuzione alla studio della Phyllactinia corylea. Nuovo Giornale Botanico Italiano 12: 313–327. 1905.
167. **Wagner, G.** Culturversuche mit Puccinia silvatica Schroeter auf Carex brizoides L. Hedwigia 34: 228–231. 1895.
168. —— Beiträge zur Kenntnis der Coleosporien und der Blasenroste den Kiefern (Pinus silvestris L. und P. montana Mill.). Zeitschr. f. Pflanzenkr. 6: 9–13. 1896.
169. —— Beiträge zur Kenntniss der Puccinia silvatica Schroeter und der Puccinia sessilis Schneider. Ber. d. d. Bot. Gesell. 14: 212–215. 1896.
170. —— Beiträge zur Kenntniss der Coleosporien und der Blasenroste der Kiefern (Pinus silvestris L. and Pinus montana Mill.) III. Zeitschr. f. Pflanzenkr. 8: 257–262. 1898.
171. **Ward, H. M.** On the Relations between Host and Parasite in the Bromes and their Brown Rust, Puccinia dispersa Erikss. Ann. Bot. 16: 233–315. 1902.
172. —— Further Observations on the Brown Rust of the Bromes, Puccinia dispersa (Erikss.) and its Adaptive Parasitism. Annales Mycol. 1: 132–151. 1903.
173. —— Experiments on the Effect of Mineral Starvation on the Parasitism of the Uredine Fungus Puccinia dispersa on Species of Bromus. Proc. Roy. Soc. (London) 71: 138–151. 1902.
174. —— Recent Researches on the Parasitism of Fungi. Ann. Bot. 19: 1–54. 1905.

# RELATION OF MARL PONDS AND PEAT BOGS

W. W. ROWLEE

*Cornell University*

The filled-in lakes and ponds of western New York are of two distinct types, the bogs often called peat or cranberry bogs, and the marl ponds. These ponds are alike in that both occupy depressions in the terrain and both are filled with water from springs at their bottom or near their shores. They also resemble each other in that both are subject to filling in with material produced by organic life in and around them. They differ from each other however in the character of the water they contain, in the flora which inhabits the water and the adjacent shore and the method by which they are filled in.

The glaciation of the country left a terrain with potholes and other depressions particularly favorable to peat-bog formation.

The material with which peat bogs are filled consists mainly of sphagnum and heath-like plants always much disintegrated and accumulated principally around the shores. Peat bogs have long been a subject of interest. Mitchill in 1798 studied them and set forth their general structural characteristics in a paragraph of his report as commissioner for the Agricultural Society of New York, as follows: "As the peat is formed, layer over layer, in the course of successive vegetations, it can be easily explained how trunks of trees, fossil wood, and bodies and bones of animals came to be buried so deep below the present surface; because at the same time when the trees fell, and animals died, in the places where they are now found, they were upon the top, and, by the perpetual growth of the plants around, they have in many places, become covered to a great depth." He was particularly impressed with the bones of extinct species of animals found in bogs in Orange County and other parts of eastern New York. Dachnowski in 1912 gives a very comprehensive discussion and classification of the distribution of species in the several areas on the surface of a bog.

The flora now found on the peat bogs corresponds to the flora of colder climates. The flora of the marl ponds corresponds more closely to that of the seashore in the same or more southerly latitudes. Marl ponds are filled in not only near the shores but in all parts of the pond where the water is not too deep. The water in the marl ponds is

decidedly hard, that is, it is impregnated with lime while the water of peat bogs is soft, that is, it is not alkaline in its reaction.

In a series of careful studies Davis has shown that marl is composed mainly of the remains of the alga *Chara*. *Chara* thrives in hard water and its cell walls are impregnated with calcium carbonate. In many marl ponds a complete transition from the living *Chara* to characteristic marl can be seen. Since *Chara* grows submerged and the principal bog plants grow emerged it is evident why there is filling at the shore in the one and in all parts of the pond in the other.

In sounding many peat bogs in western New York, the writer was somewhat surprised to find many of them underlayed with marl.

FIG. 1. Marl bog, northeast side of Lowry's Pond, West Junius, Seneca Co., N. Y. Species of sedges the dominant vegetation form.

The assumption had been that the alkaline or nonalkaline character of the water originally filling the depressions determined whether bog vegetation or marl pond vegetation would develop in it. Is it possible that a pond might be alkaline during one stage of its existence and then become non-alkaline in a later stage? An affirmative conclusion seems inevitable.

It is Dachnowski's view that there are changes in the vertical or historical succession in the bogs, for he says: "While working on the ecology of ravines near Ann Arbor, Michigan, I became convinced that the reactions of plants on their habitat were equally as great and profound, in some cases, as the influence of edaphic and climatic

factors. In various places the decomposed remains of an earlier vegetation led to mechanical and chemical changes in the soil, the extent of which was more effective toward breaking up the flora into a heterogeneous formation, accompanied by a frequent replacement of one dominating group by another."

There are some bogs without evidence of marl at the bottom. Davis reports all the many peat bogs examined by him in Maine as resting on sand, clay or rock bottom, none on marl. Most of the peat bogs in the Adirondack region of New York have no marl at the bottom. These presumably were from the first supplied by springs of non-alkaline water. Some of the peat bogs of central and western

FIG. 2. Peat bog near McLean, Tompkins Co., N. Y. *Chamaedaphne*, *Andromeda*, *Ledum* and other heaths together with *Sphagnum* form the dominant vegetation.

New York have great masses of marl under them. Such a one is near Peterboro in Madison County and another on Gorham Creek in Ontario County. Here it is apparent that some agency changed the composition of the water to such an extent that oxylophytes found conditions congenial.

The most extensive marl ponds in the region are in the vicinity of the limestone belt of central New York. They occur at West Junius in Seneca County and southwest of Rochester, especially at Bergen in Genessee County. Isolated and much smaller marl ponds

occur at Tully and near Cortland. The limestone outcrop in these regions accounts for a continuous supply of water impregnated with lime. The peat bogs with the greatest thickness of marl under them occur not far from this same limestone belt, while the peat bogs with little or no marl are usually farthest from the limestone outcrop.

It does not seem at first thought as though *Chara* could be the agency causing the radical change in the history of the vegetation of the pond and the accumulations in these depressions. In so far as vegetation is concerned calcium carbonate is relatively insoluble.

FIG. 3. Transition bog near Cortland, N. Y. A thick bed of marl is overlaid with about four feet of fibrous peat. Marl was excavated from the hole in the foreground. Sedges are prominent in the vegetation now covering the surface of the bog.

Not so, however, is the lime in spring water. The water with available (more or less) free lime is what *Chara* takes in and in its life processes converts into calcium carbonates secreted in its walls. That an immense amount of lime is converted is shown by the bulk of marl in the ponds. Where the amount of the lime in the original soil was not large, rain water constantly tended to wash it out and in the course of time the lime content of the water would be decreased. The ponds were artesian pools fed by these springs and as the character of the water changed there was, if our theory is correct, a corresponding

change in the flora. There would be then two phases in the life of our bogs.

*1st.* The marl ponds in which lime-loving plants predominated and especially *Chara* and which are filled with and often surrounded by beds of marl or "bog lime."

*2nd.* Peat bogs which from the bottom up are composed of non-alkine peat which in all their history have been inhabited by oxylophytes.

Between these two phases gradations of all degrees occur in the peat bogs of western New York. The succession might, of course, be in the other direction if the calciferous phase should become predominant over a previous carboniferous one. But such a case is unknown in western New York.

# PATHOLOGICAL PROBLEMS IN THE DISTRIBUTION OF PERISHABLE PLANT PRODUCTS[1]

C. L. SHEAR

*Bureau of Plant Industry, U. S. Department of Agriculture*

## Introduction

Under our present social and economic conditions, public interest is being aroused and directed to questions and problems which have been largely overlooked or neglected in less strenuous times. The conservation of our natural resources, especially our food products, greatly to our discredit as a nation, has, until very recently, been too largely neglected. Max O'Rell is said to have made the statement some years ago that Europe could be fed on what America wastes. This statement is probably somewhat exaggerated, but unfortunately has too many facts to support it.

At present, these questions, so far as food products are concerned, are of *vital* importance, not merely figuratively but literally. We wish to call attention here to loss and waste occurring in connection with the distribution of fruits and vegetables.

A large proportion of the fruit and truck crops grown never reach the consumer. Part of this loss occurs on the farm and in the orchard, and part in transit and distribution. Adams[2] in his recent work on marketing perishable farm products, asserts that at least 25 percent of the perishables which arrive at the wholesale markets is hauled to the dump pile because it is unfit for human consumption. This statement we fear is not based upon sufficient data to be accepted. It is, however, the opinion of one writer on the subject.

In 1910, according to Dr. Pennington,[3] the New York Board of Health condemned and destroyed over twelve million pounds of fruit and over seven million pounds of vegetables. This presumably does not represent the total loss, as a considerable amount probably escaped detection. It is easy to see that such great destruction of food

[1] Published by permission of the Secretary of Agriculture.

[2] Adams, Arthur B. Marketing perishable farm products. Studies in history, economics, and public law, Columbia University. 72[3]: 25. New York. 1916.

[3] Pennington, Mary E. Proper handling of foodstuffs from farm to market. In Report of the Mayor's Market Commission of New York City, p. 257, New York, 1913.

products must be a serious drain on our food supply and must add materially to the cost of living. No adequate estimate can, however, be made of the enormous economic loss represented in such cases. Think of the time, labor, and investment involved in the planting, cultivating, harvesting, and hauling of these products, and of the freight or express, refrigeration and delivery charges paid! This is one of the most expensive forms of economic loss imaginable.

## Causes of Losses

The important problems which confront investigators, producers, carriers, and consumers, are the causes and means of prevention of these enormous losses. The producers and transportation companies have heretofore been too much inclined to look upon their share of these losses as among the natural hazards of their business. The carriers, however, are now realizing more fully than ever before, the great reduction in their income due to the payment of claims from shippers for loss resulting from decay and spoilage of products in transit. According to the report of the American Association of Refrigeration,[4] the total amount of claims paid by 180 railroads in 1914 for loss of perishable freight was $4,977,383.09; of this amount over one half, or $2,687,393.36 was for fruit and vegetables. This, of course, does not represent all the railroads of the country nor all the losses on the roads represented.

In order to devise means of reducing or preventing this enormous destruction of food products, it is, of course, first necessary to determine the causes and their relations and importance. The deterioration of fruits and vegetables in transit is due chiefly to the action of parasitic or saprophytic fungi. Natural ripening processes and changes in the cell contents caused by the accumulation of respiration products or smothering, may also render the articles unfit for food. These changes are usually hastened by high temperature and lack of ventilation. Each kind of fruit has, of course, its own natural keeping qualities. Some kinds, like strawberries, raspberries, blackberries, and figs, soon become spoiled under optimum conditions, while others, like apples, may be kept in good condition for relatively long periods. The structure and composition of the ordinary perishable plant products and their relations to the keeping and carrying qualities of such products are fairly well known and no discussion of them will be attempted here.

There are many other factors, however, involved in determining the keeping and carrying qualities of fruits and vegetables, such as

[4] Bulletin No. 2. Issued by Commission on Railway and Steamship Refrigeration of the American Association of Refrigeration, p. 82, June, 1916.

soil and climatic conditions under which they are grown, methods of cultivation and fertilization, nature of the variety, condition as to maturity at time of harvesting, methods and care in harvesting, grading, packing, and handling previous to shipment, and methods of loading, stowing, and bracing in the cars. Any or all these factors may be and frequently are involved in the final decay due to parasitic or saprophytic fungi occurring in the field or in transit. Hence it is of the utmost importance to obtain as complete knowledge as possible of the various organisms which attack the particular product, their life histories, the time, mode, and conditions of infection and development and also their relations to methods of handling and their temperature, moisture, and host relations. These problems are primarily pathological.

Growers and shippers long ago discovered that storing fruits and vegetables at low temperature prolongs their keeping. This observation finally led to the development of commercial cold storage and refrigeration methods and practices. These methods and practices have developed thus far largely along empirical lines. It happens that growth in most of the organisms which destroy perishable plant products is inhibited at from 33° to 36° F. Therefore, if fruit or vegetables, though infected with fungi, are placed under such temperature conditions before development of these organisms is too far advanced, growth of the fungi will be temporarily suspended. In some cases, therefore, refrigeration may simply delay the destruction of the product and shift or render uncertain the responsibility for its loss which may occur before it reaches the consumer.

It will appear evident, therefore, that in order to devise methods of preventing or avoiding such losses, all the factors involved in any particular case must be accurately determined as well as their relations and relative importance. Because it is known that certain fungi destroy certain fruits and vegetables and that these fungi occur in the orchard or on the farm, it has been inferred by some that the presence of such organisms on decayed products at destination is sufficient evidence that the responsibility for the loss rests with the grower. This may be true in the case of some particular product affected with some particular disease when shipped without refrigeration. In the case of refrigerated products, however, our experience and that of others has shown that in order to determine the real cause or causes and the responsibility for loss in any specific case, the whole history of picking, packing, handling and treatment of the product must be known, or at least its history from the field to destination. This has been very strikingly brought out in the investigations of

citrus fruits and also in recent investigations of raspberry, strawberry, and cranberry losses.

The practice of refrigeration of fruits and vegetables in transit is for two purposes, viz.: to retard the natural ripening processes which continue after the crop is harvested and to prevent the development of destructive fungi which are assumed to be present and are likely to develop unless a constant low temperature is maintained. In many cases it is practically impossible to eliminate the organisms which cause decay and all the handling in such cases must be with the presumption of their presence and the possibility of their rapid development under favorable conditions.

Each product and each fungus has its own peculiarities and reactions under various conditions and treatment. This may be illustrated by citing a few specific cases.

### Stem-End Rot and Anthracnose of Watermelon

Meier[5] has given an account of a decay of watermelons in the field and in transit, caused by a species of *Diplodia*. It has been found that this organism is a wound parasite, and infection takes place through the stem end of a melon after it has been cut from the vine. A practical method of preventing this infection by the application of a fungicide before shipment has been found to be the simplest means of preventing decay from this cause. The anthracnose of watermelons can also be largely controlled by proper field treatment.

### Leak of Potatoes

This trouble, which is most prevalent on the Pacific coast, has been found by Hawkins[6] to be due chiefly to *Pythium debaryanum*. It has been shown that infection occurs in the field and through wounds only; hence, the most practical means of prevention is to avoid as much as possible injury in digging and handling and to sort out all wounded potatoes before shipping. This is a case in which transportation methods and facilities are not the controlling factor in determining the condition of the product upon its arrival in the market, but are of minor importance.

Potatoes, watermelons, and similar products which are not usually shipped under refrigeration can fortunately be more or less satisfactorily insured against loss by proper treatment previous to shipment. The temperature, ventilation and handling of such products

[5] Meier, F. C. Watermelon stem-end rot. Journal of Agricultural Research 6: 149–152. Ap. 24, 1916.

[6] Hawkins, Lon A. The disease of potatoes known as "Leak." In Jour. Agri. Res. 6: 627–640. 1 fig. pl. XV. 1916.

en route, however, have considerable influence upon their condition at destination, even when all practical field treatments and precautions have been taken.

### Citrus Fruits

In the case of citrus fruits, it has been found that where the chief cause of decay is *Penicillium*, one of the important factors in its control is to avoid, as far as possible, all injury to the fruit in picking and packing, as the fungus enters only through wounds. It is also necessary to ship this fruit under proper refrigeration in order to insure its arrival in good condition in distant markets. While proper care in picking, packing, and handling are of primary importance in determining the keeping qualities of these fruits, proper refrigeration and prompt delivery are also essential to prevent loss from this and other organisms.

### Cranberry Rots

Cranberries under proper conditions of cultivation and handling possess excellent shipping and keeping qualities and as they are mostly distributed during cool weather do not require refrigeration. Spraying to prevent fungous diseases in the field, careful picking and handling with temporary storage in cool ventilated houses and packing in proper packages will ordinarily insure their reaching market in good condition with the usual means of transportation. Most of the losses occur before shipment and much loss of fruit held for late shipment is due to the natural ripening processes of the fruit, the action of the respiration products and smothering. Proper ventilation would prevent the latter.

### Raspberry Rots

Ramsey[7] reports the results of studies of shipments of raspberries from the Pacific coast under various conditions. The decay was attributed to *Botrytis* and *Penicillium*. He found that care in handling and prompt cooling were among the most important factors in successful shipment, but that maintaining a uniform low temperature in transit was also essential.

### Strawberry Leak

In the cases of strawberries which have been investigated by Stevens and Wilcox,[8] of the Bureau of Plant Industry, for the past

[7] Ramsey, H. J. Factors governing the successful shipment of red raspberries from the Puyallup Valley. U. S. D. A. Bul. 274: 1915.

[8] Stevens, N. E., and Wilcox, R. B. *Rhizopus* rot of strawberries in transit. U. S. D. A. Bull. 531: 4–7. 1917.

two years, it has been found that "leak," a decay caused by *Rhizopus*, which is the most rapid-growing destructive organism attacking this fruit, can be controlled by proper methods of picking, handling, and shipping. *Rhizopus* spores seem to be practically omnipresent and it is impossible to eliminate them. All handling of strawberries must, therefore, be based upon the assumption of their presence. The fungus, however, cannot gain entrance through the uninjured tissues and does not develop seriously at a temperature below 45–50° F. Southern-grown strawberries having fair natural shipping qualities, carefully picked and handled, and not subjected to too high temperatures before shipment, can with proper refrigeration and transportation be delivered in northern markets in good condition. If a carload of strawberries shows much "leak" at destination, it may be due to delay or rough handling of cars in transit, and faulty refrigeration; or it may be due to improper treatment by the grower or shipper. Only a full knowledge of all the facts in any particular case can determine the exact cause or causes and responsibility. The presence of the fungus on the fruit at destination is not sufficient to throw the blame on the grower or shipper.

### Brown Rot of Peaches

The brown-rot fungus, *Sclerotinia cinerea*, which is one of the most serious causes of decay of peaches, is very common and widely distributed and is found in practically all peach orchards in humid regions. It is doubtful whether a shipment of peaches grown in such a region could be found which did not contain spores of this organism. Notwithstanding the general presence of this fungus on peaches, if the fruit is picked at the proper stage of development, and properly handled, packed and refrigerated in transit, such fruit may, and usually does, reach distant markets and the consumer in good condition. The fact that a carload of peaches arrives at destination in a decayed condition and the brown-rot fungus is present, does not necessarily indicate that the grower is to blame for the loss.

Mr. J. A. Ruddick,[9] Canadian Dairy and Cold Storage Commissioner, states that Canadian peaches from the Niagara district are successfully shipped from Canada to Liverpool and London, the time in transit to London being twelve days, and also that in 1910 twenty-three thousand cases were shipped from Cape Town, South Africa, to London, arriving in good condition. Seventeen days was the minimum time in transit. Other shipments from the same place

[9] Ruddick, J. A. Cold storage for apples and other fruit. Evidence of Mr. J. A. Ruddick before the Select Standing Committee on Agriculture and Colonization, 1910–11, pp. 106–109. Ottawa, 1911.

were made to Canada by way of New York, also arriving in good condition and selling at one shilling each. This indicates some of the possibilities of shipping such a perishable fruit as the peach when properly handled and treated, even though "inherently liable to deterioration and decay."

Stevens,[10] citing the fact that peaches become infected with the brown-rot fungus only in the orchard or before shipment, says: "We may be sure that if infected at destination, shipment was also infected at the starting point. It appears clear to the writer that in both these cases (*Sclerotinia libertiana* on lettuce being the other case mentioned) the responsibility rests with the shipper just as much as it would if a consignment of horses infected with glanders but not yet showing the disease was placed upon the cars."

We have been unable to discover facts or data to support the statement that in such fruit responsibility for losses in transit rests entirely with the shipper. Investigations have shown that the brown-rot fungus makes little or no growth at a temperature of 32–35° F. (0–2° C.),[11] and that if the fruit is kept at this temperature brown rot does not develop. Of course, all practical field treatment to reduce infection should be practiced.

As a result of the above quoted and similar statements some railroad representatives have taken the position that the presence in a shipment of spoiled fruit or vegetables at destination of destructive fungi known to originate in the field, is sufficient to justify the conclusion that the carrier is free from any responsibility for the loss. Such a general conclusion as this is not in accord with the facts and is fraught with great possibilities of injustice. Every effort should be made to correct this mistake. In the past the transportation companies have undoubtedly paid many unjust claims. Now there seems to be danger of the pendulum swinging to the other extreme, resulting in the rejection of just claims.

It is possible for transportation companies to prevent any just claims for losses due to destructive fungi by furnishing proper cars and refrigeration service and delivering the products on schedule time. With the recent improvement of refrigerator cars a sufficiently uniform low temperature throughout the load can be maintained to avoid the trouble which so frequently occurs of having variations in temperature, of 20 degrees or more, between the top and bottom of the car, as reported by Ramsey.[12] Under such conditions decay

[10] Stevens, F. L. Some problems of plant pathology in reference to transportation. Phytopathology 5: 108. Ap. 1915.

[11] Brooks, Chas. and Cooley, J. S. Temperature relations of apple-rot fungi. Jour. Agr. Res. 8: p. 163, Jan. 1917.

[12] Ramsey, H. J., l. c.

and loss in some products are sure to occur, no matter how great care has been given them before shipment.

The grower and the shipper, however, are subject to many hazards and conditions, some of which are beyond their control. Chief among these are climatic factors. There are many things, however, which can be done by the producer to prevent or reduce losses of this kind. All practical means of prevention should be utilized and as soon as the cause of the trouble in any specific case is determined, every reasonable and practicable effort should be made by the producer or shipper to remove such cause. On the other hand, the carrier should modify and improve his equipment and methods when necessary to insure the delivery of perishable products in a sound condition.

The various cases described above show something of the variety and complexity of the problems involved and the need of thorough investigations to discover the causes and remedies in each case.

The numerous factors involved in the case of any two products or diseases are frequently not the same and when they happen to be the same are not of equal importance. Most of them are primarily pathological or have very direct pathological bearings. Where fungi are concerned, as in most cases, full knowledge must be obtained of their host relations, time, mode and conditions of infection, temperature and moisture relations and the effect on their development of various methods of treatment of the fruit or vegetable during its production, harvesting, packing, handling and transportation.

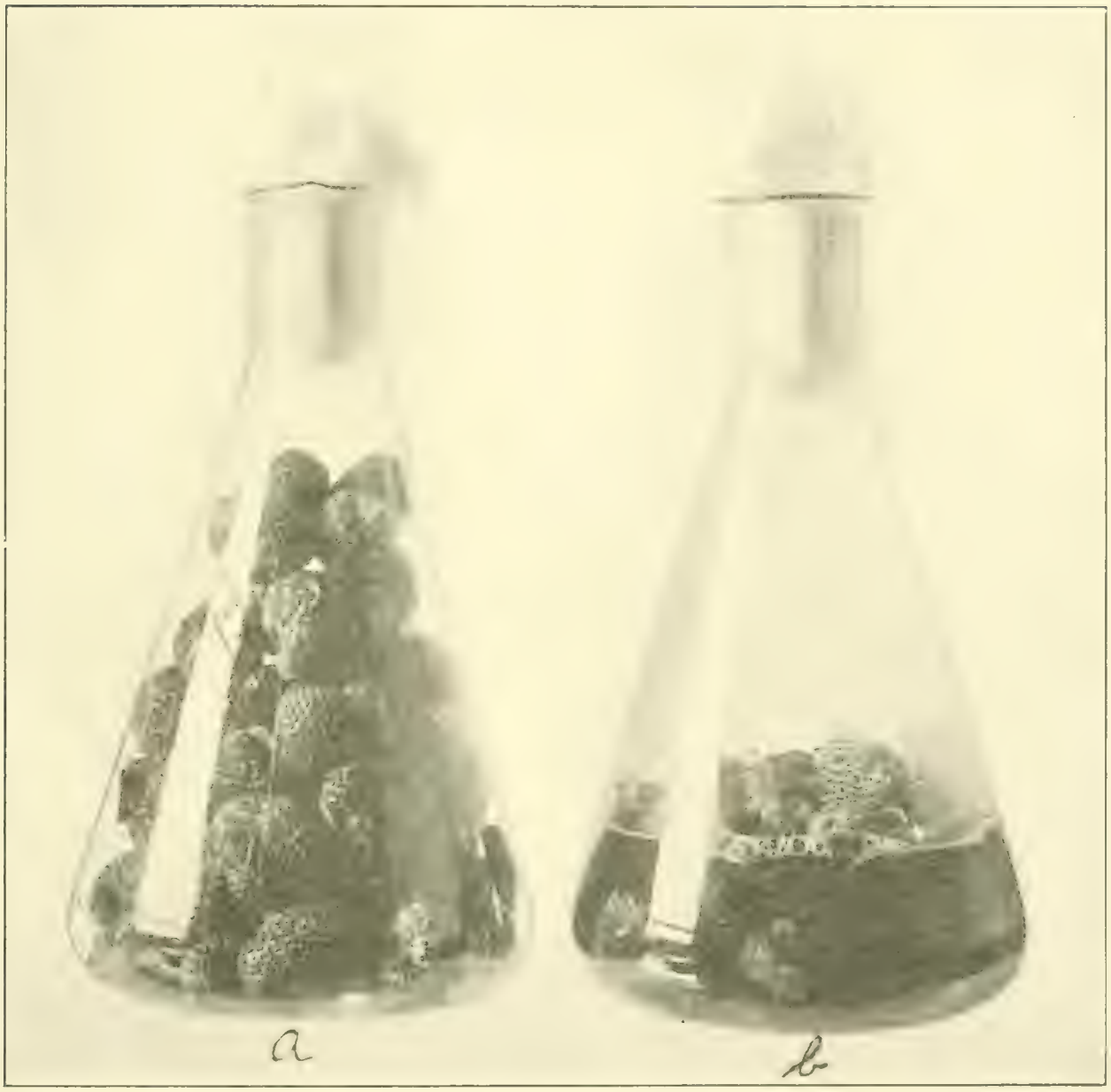
The present agencies interested in and at present studying these problems are the pathologists, pomologists, horticulturists, refrigeration engineers, the specialists in markets and marketing, the railway freight claims associations, and the commercial inspection services. The most complete cooperation of all these agencies is necessary in order to solve these important problems most quickly and thus reduce as far as possible this great economic loss.

## EXPLANATION OF PLATES IX–XI

PLATE IX. Two flasks of Missionary strawberries kept two days at ordinary room temperature. *a*. Containing fruit in natural condition free from wounds. *b*. Containing same quantity of fruit inoculated with *Rhizopus*.

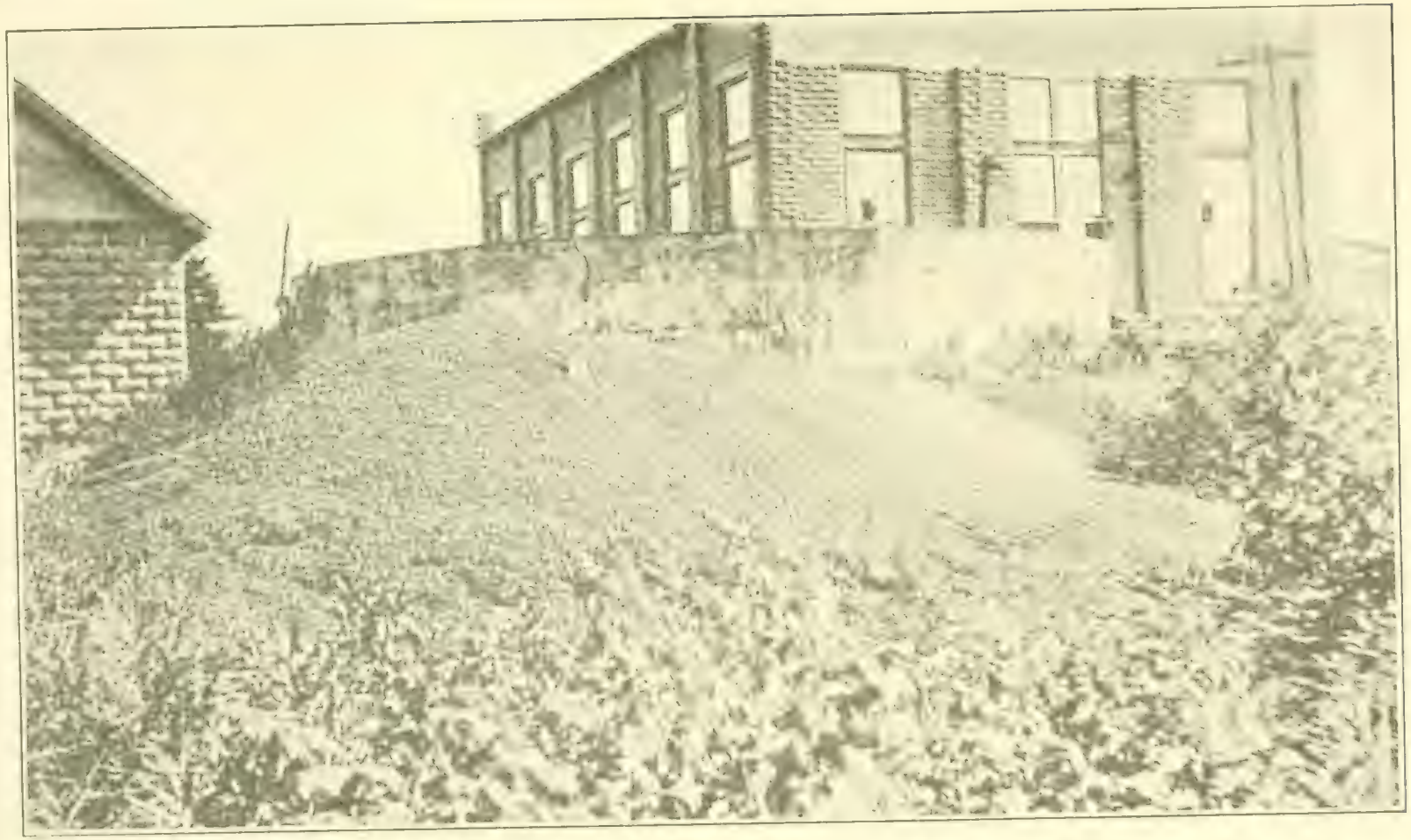
PLATE X. Three wounded strawberries above; three sound berries below. All were sown with spores of *Rhizopus*. Photographed after two days at ordinary room temperature. The three wounded berries entirely destroyed, the three others sound.

PLATE XI. Pile of spoiled cranberries discarded in sorting and screening. Loss chiefly due to fungous disease and to the effect of ripening processes and their products or smothering.




SHEAR: STRAWBERRY LEAK

SHEAR: STRAWBERRY LEAK



SHEAR: CRANBERRY ROTS

# TUBERS WITHIN TUBERS OF SOLANUM TUBEROSUM

F. C. STEWART

*New York State Agricultural Experiment Station, Geneva*

At the New York Agricultural Experiment Station, in 1915, several bushels of seed potatoes not needed for the spring planting were left over summer in a cellar. The potatoes were of the variety Sir Walter Raleigh. They were stored in slatted crates which were piled one above another three crates deep in a single row along the cellar wall. The cellar was cool, moderately damp and dimly lighted. Its floor and walls were of cement.

FIG. 1. A new tuber protruding from a slit in the side of an old seed tuber of *Solanum tuberosum*. Nat. size.

No attention was given the potatoes until the latter part of September. It was then observed that instead of producing sprouts in the usual manner they had formed large numbers of new tubers. Some of the new tubers were in sessile clusters of several small tubers

each while others were borne singly on sprouts one to three centimeters long and were of considerable size.

The formation of new tubers directly from old ones in this manner is so common as to attract little attention. The unusual features of the present case were: (1) The large size of the new tubers. Many of them had a weight of 25–30 grams, several of 50–60 grams, and one weighed 67 grams. (2) The formation of new tubers within old

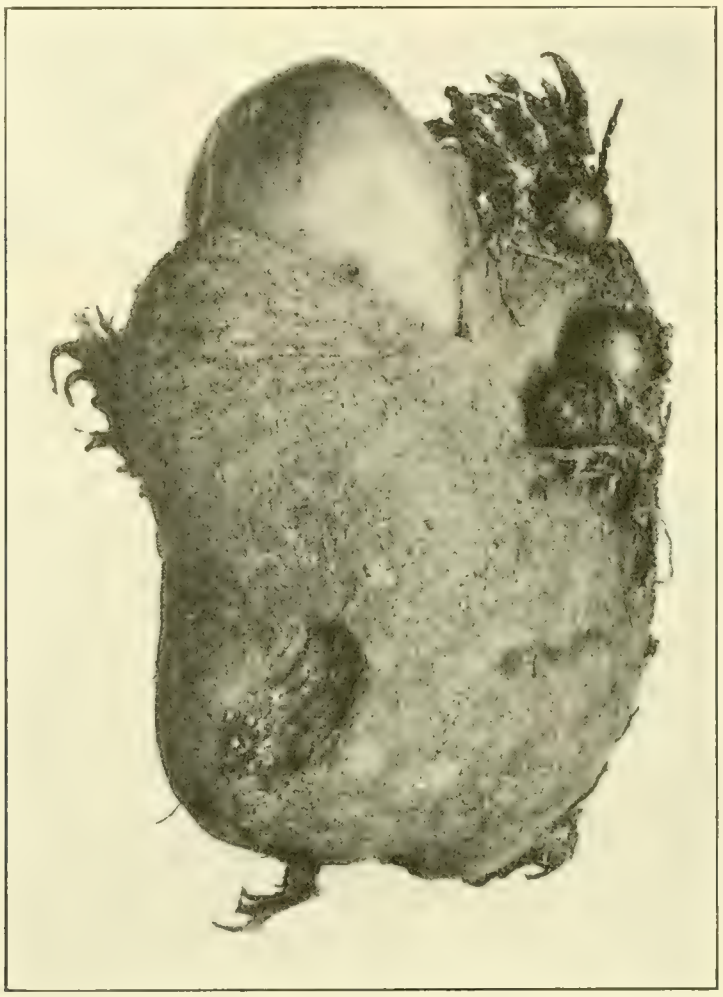


FIG. 2. A new tuber protruding from a slit at the bud end of an old seed tuber. Nat. size. (Compare Fig. 3.)

ones. Fifteen of the old tubers had large new tubers protruding from slits in their sides (Figs. 1–2). In one instance a new tuber weighing about 28 grams was wholly included within the parent tuber. This, like most of the protruding new tubers, was considerably flattened by the pressure to which it had been subjected during its growth.

This phenomenon of large new tubers within old ones was a sight calculated to excite wonder in the beholder. To the mycologist it suggested the bursting of the volva in the egg stage of the phalloids.

To one familiar with Gager's interesting paper[1] on ingrowing sprouts of potato tubers it appeared probable that tubers forming on ingrowing sprouts had enlarged until the pressure produced became sufficient to rupture the tissues of the parent tuber. Upon dissection of the tubers this was found to be true.

FIG. 3. The specimen shown in Fig. 2 with one side cut away to show the origin of the ingrowing sprout which bears the new tuber. A slight change in pose has brought to view a second new tuber. Nat. size.

The old tuber shown in Fig. 2 was carefully dissected to determine the origin of the sprout bearing the new tuber which was emerging from a slit at the bud end. It was found to have started from the "eye" on the right side of the old tuber where the two external, sessile new tubers are seen. Fig. 3 shows the same tuber, in a slightly different position, with the tissue cut away so as to expose the new tuber and the sprout bearing it. In accomplishing this one of the

[1] Gager, C. Stuart. Ingrowing sprouts of *Solanum tuberosum*. Bot. Gaz. 54: 515–524. 1912.

small external tubers was removed. The changed pose in Fig. 3 brings to view a second new tuber not shown in Fig. 2.

The larger of the new tubers was borne on a very short branch three centimeters from the point of origin of the sprout; and the smaller one on a similar branch about a centimeter beyond. The course of the ingrowing sprout was perpendicular to the surface of the parent tuber at the point of origin. Apparently, the direction of growth had been inward from the beginning. Close observation of this and some other specimens revealed nothing to indicate that the sprouts had started externally and turned inward. Whether it was the tip of the sprout or the expanding tubers which first broke through the cortex cannot be determined in this case; but in other specimens (among them the one shown in Fig. 1) it was clear that the new tuber had been responsible for the rupture of the cortex.

The ingrowing sprouts exhibited the lenticel-like openings observed by Gager. These signify nothing except that the sprouts were formed in a humid atmosphere. The fibrous roots observed by Gager were lacking and the sprouts were but slightly branched.

The strange behavior of these tubers cannot be ascribed to low vitality. This is shown by the fact that a large number of tubers from the same lot were planted and a good stand of vigorous plants obtained.

In the main, these observations agree with those made by Gager and add nothing to them except to show that tubers of considerable size may form on ingrowing sprouts and produce a striking freak of nature. The internal tubers observed by Gager were small ones.

# THE DUPLICATION OF A LEAF-LOBE FACTOR IN THE SHEPHERD'S-PURSE[1]

GEORGE HARRISON SHULL

*Princeton University*

In two previous papers (Shull, 1911, 1914) I have demonstrated the existence of two independent Mendelian factors in the shepherd's-purse (*Bursa bursa-pastoris*), each of which produces the triangular form of capsule. In the latter paper I discussed at some length some of the criteria and the significance of such "duplicate" factors. I gave also a practically complete list of the relevant literature which had appeared before 1914, and called attention to certain misconceptions which had found expression in a number of the papers cited.

It is not necessary, therefore, in presenting a new case of duplication of factors in this species, to repeat at any length the discussion in this earlier paper. It is important however to direct attention to the discussions there presented, since several papers along similar lines, or on closely related matters, which have appeared more recently, do not include a reference to my paper, even when from the terminology used it is evident that the authors have had it before them. Several writers are now making the desired distinction between "duplicate" and "plural" factors, and it is to be hoped that in the future, in the interest of precision and accuracy, all those who discuss size-inheritance and related phenomena, will abandon the expression "multiple" factors because of its erroneous implications.

It has been shown (Shull, 1909, 1910, 1911) that the form of leaf in shepherd's-purse is controlled by certain Mendelian genes which have been designated *Aa* and *Bb*, the presence of *A* resulting in an elongation of the primary lobes of the leaf, while the *B* gene divides the leaf to the midrib, and brings to light certain characteristic secondary lobing. The several possible combinations of these genes give the four rosette types: *AB* = *heteris*, *aB* = *rhomboidea*, *Ab* = *tenuis*, and *ab* = *simplex*. These four forms are illustrated in Figs. 1–4.

I have now studied the progenies of a considerable number of wild Bursas from places as diverse as Chile, Hawaii, Japan, China,

[1] Contribution from the Station for Experimental Evolution, of the Carnegie Institution of Washington, and from the Genetical Laboratory of Princeton University.

(171) (172)

FIG. 1.—*heteris.*

(183) (184)

FIG. 2.—*rhomboidea.*

(301) (302)

FIG. 3.—*tenuis.*

(303) (304)

FIG. 4.—*simplex.*

FIGS. 1–4. Climax leaves from eight rosettes representing the four phenotypes in pedigree No. 15406. *Heteris* and *rhomboidea* possess one or more *B* factors; *tenuis* and *simplex* lack them.

Australia, Tasmania, India, Ceylon, South Africa, the Sahara, and from widely distributed points in Europe and North America, and find that the forms everywhere fall into one or more of these four rosette types. This does not mean, however, that with respect to leaf-form there are only four biotypes of this species in existence, for nearly every lot of material from a new locality presents minor details of lobing which lead to their easy recognition as new and distinct biotypes.

In all of the earlier crosses between types respectively dominant and recessive for either of the above-mentioned character-pairs, there appeared in the $F_2$ close approximations to the monohybrid ratio, 3 : 1, or undoubted modifications of that ratio,—the modifications being due, in most cases at least, to the facts (*a*) that the *A* factor has been in some combinations not completely dominant, and (*b*) that both *A* and *B* require for their manifestation a certain *minimum opportunity* in the way of favorable environment, including cultural treatment.

These results having been well established while the situation in regard to the capsules called for further extensive investigation, a number of my cultures which concurrently involved the rosette characters and the capsule characters, have been grown under conditions not ideal for the development of the leaf lobes, though adequate for the determination of capsule form. For this reason my records with respect to the leaf types in certain families are of such incompleteness as to make the recorded ratios of no particular value. In nearly all cases, however, a small portion of each pedigree has been given sufficiently good treatment that the composition of the several families with respect to the rosettes could be inferred with small probability of error.

The discovery to be detailed below, that in certain races there are two independent Mendelian factors which affect the leaf-form in identical ways, each dividing the leaf to the midrib and bringing out the secondary lobing which is seen unmodified in *rhomboidea* and modified by the action of the *A* factor in the case of *heteris*, has revived my interest in the inheritance of the rosette characters and investigations are now in progress which I hope will give in time a full insight into the composition of the rosettes with respect to the major factors affecting the leaf lobes.

The duplication of the gene which produces the triangular capsule has been found almost universally distributed geographically, as will be shown in detail in a later report, but the duplication of the leaf-lobe factor, *B*, appears to be relatively much less frequent.

Before presenting the evidence of dimery in respect to the *B* lobes of the leaves, it will be advantageous to have before us the

cases of monomery with respect to this character, as indicated by the occurrence of monohybrid ratios in the $F_2$ from crosses between plants respectively having and lacking the characteristic "*B*"-lobing.

TABLE 1

*Composition of $F_2$ Families which Show Monohybrid Ratios, from Crosses Involving the Presence of the B Factor in Wild Biotypes of Shepherd's Purse*

| Origin | Pedigree Numbers | | | *heteris AB* | *rhomboidea aB* | *tenuis Ab* | *simplex ab* | Ratio *B:b* |
|---|---|---|---|---|---|---|---|---|
| | $P_1$ | $F_1$ | $F_2$ | | | | | |
| New Carlisle, Ohio | — | 040 | 054 | 114 | 53 | 47 | 16 | 2.65 : 1 |
| | 040 | 056 | 06130 | — | 217 | — | 72 | 3.01 : 1 |
| | 13148 × 1376 | 14359 | 15361 | 194 | 58 | 43 | 30 | 3.45 : 1 |
| | | | 15362 | 81 | 17 | 26 | 8 | 2.88 : 1 |
| | | | 15363 | 163 | 70 | 44 | 46 | 2.58 : 1 |
| Chicago, Illinois | — | 040 | 0514 | 99 | — | 26 | — | 3.81 : 1 |
| | 0515 | 0693 | 07203 | 94 | — | 37 | — | 2.54 : 1 |
| Cardiff, Wales | 1337 × 1338 | 14357 | 15356 | — | 50 | — | 9 | 5.55 : 1 |
| | | | 15357 | — | 167 | — | 85 | 1.96 : 1 |
| | 13214 × 13179 | 14361 | 15367 | — | 20 | — | 8 | 2.50 : 1 |
| | | | 15368 | — | 49 | — | 18 | 2.72 : 1 |
| | | | 15369 | — | 28 | — | 15 | 1.87 : 1 |
| Groningen, Holland | 1315 × 1376 | 14348 | 15324 | 164 | 54 | 31 | 10 | 5.32 : 1 |
| | | | 15325 | 40 | 10 | 11 | 2 | 3.84 : 1 |
| | | | 15326 | 40 | 7 | 4 | 3 | 6.71 : $1^2$ |
| | 1317 × 1376 | 14349 | 15327 | 24 | 5 | 3 | 0 | 9.67 : $1^2$ |
| | | | 15328 | 128 | 49 | 48 | 18 | 2.68 : 1 |
| | 1317 × 1338 | 14350 | 15329 | 103 | 43 | 22 | 6 | 5.21 : 1 |
| | | | 15330 | 187 | 35 | 54 | 9 | 3.52 : 1 |
| | 1319 × 1338 | 14352 | 15331 | 24 | 11 | 3 | 1 | 8.75 : $1^2$ |
| | | | 15332 | 28 | 18 | 10 | 4 | 3.29 : 1 |
| | | | 15333 | 108 | 33 | 20 | 13 | 4.27 : 1 |
| | 1333 × 1376 | 14353 | 15334 | — | 147 | — | 68 | 2.16 : 1 |
| | 1335 × 1376 | 14355 | 15340 | — | 104 | — | 39 | 2.67 : 1 |
| | | | 15341 | — | 66 | — | 17 | 3.88 : 1 |
| | | | 15342 | — | 11 | — | 8 | 1.37 : 1 |
| | 120 | 13219 | 14523 | — | 141 | — | 47 | 3.00 : 1 |

TABLE 1 (*continued*)

| Origin | Pedigree Numbers | | | *heteris* *AB* | *rhomboidea* *aB* | *tenuis* *Ab* | *simplex* *ab* | Ratio $F_2$ |
|---|---|---|---|---|---|---|---|---|
| | $P_1$ | $F_1$ | $F_2$ | | | | | |
| Berlin, Germany | 13218 × 1376 | 14365 | 15373 | — | 186 | — | 73 | 2.55 : 1 |
| | | | 15374 | — | 48 | — | 8 | 6.00 : 1 |
| | | | 15375 | — | 85 | — | 16 | 5.31 : 1 |
| | 13222 × 1376 | 14368 | 15382 | 3 | 230 | — | 91 | 2.56 : 1 |
| | | | 15383 | 184 | 68 | 34 | 38 | 3.50 : 1 |
| | 13223 × 13208 | 14370 | 15385 | 2 | 9 | 1 | 2 | 3.67 : 1 |
| | | | 15387 | 34 | 11 | 5 | 6 | 4.09 : 1 |
| | 13226 × 1376 | 14373 | 15394 | — | 135 | — | 35 | 3.86 : 1 |
| | | | 15395 | — | 245 | — | 71 | 3.31 : 1 |
| | | | 15396 | — | 246 | — | 80 | 3.08 : 1 |
| Landau, Germany | 056 × 059 | 0688 | 06212 | 336 | 71 | 109 | 21 | 3.13 : 1 |
| | 059 × 056 | 0689 | 06196 | 103 | 34 | 37 | 14 | 2.69 : 1 |
| | | | 06197 | 1177 | 315 | 344 | 79 | 3.29 : 1 |
| | 11498 × 11425 | 12347 | 13182 | 184 | 57 | 63 | 19 | 2.94 : 1 |
| | | 12348 | 13189 | 20 | 6 | 5 | 0 | 3.29 : 1 |
| | 11500 × 11429 | 12349 | 13190 | — | 13 | — | 3 | 4.33 : 1 |
| | | | 13191 | — | 18 | — | 2 | 9.00 : 1[2] |
| | | | 13192 | — | 116 | — | 47 | 2.47 : 1 |
| | 11503 × 11425 | 12352 | 13200 | — | 25 | — | 14 | 1.79 : 1 |
| | | | 13201 | — | 59 | — | 21 | 2.81 : 1 |
| Vicenza, Italy | — | 140 | 15586 | 43 | 5 | 9 | — | 5.03 : 1 |
| Peking, China | 13239 × 1376 | 14385 | 15420 | — | 56 | — | 6 | 9.33 : 1[2] |
| | | | 15421 | — | 33 | — | 13 | 2.54 : 1 |
| | | | 15422 | — | 25 | — | 4 | 6.25 : 1 |

All of the cases of monomeric *B* lobes which I have thus far demonstrated in wild plants are shown in Table 1.

[2] These families may possibly have a duplication of the *B* factor, but the evidence for such duplication is much less adequate than is the evidence for the occurrence of a 3 : 1 ratio in one or more $F_2$ families from these same crosses. It should be observed however, that both 15 : 1 and 3 : 1 ratios might occur in different $F_2$ families from the same cross, since the original wild plant used in the cross might have been homozygous for one *B* factor and heterozygous for the other.

Several of these ratios deviate widely from the 3 : 1 ratio, but in each such case the inclusion in the monomeric group has been based on some special consideration. In some cases one or more pedigrees from the same parentage gave a convincing approximation to the 3 : 1 ratio when grown under favorable conditions; in other cases small samples of the families have been grown under good conditions, and the inclusion of the particular pedigrees in one or another of the tables has been based upon the constitution of these small well-grown samples regardless of the indecisive ratios displayed by the family as a whole, when grown under conditions which tended to suppress the dominant leaf characters here under discussion. In still other cases a number of families belonging to later generations have been grown and have given full confirmation of the classification of the wild biotype from which the pedigree in question originated. Because of the preliminary character of the present report, it is not considered necessary to present in greater detail, the evidences in support of the conclusion that the families included in this table have a single *B* factor. It need only be stated that families whose records are indecisive for the particular point at issue, have been included for the sake of completeness, and to avoid the immorality of arbitrarily selecting for presentation those cases which are deemed to support convincingly the author's hypothesis.

Seeds of a specimen of shepherd's-purse, received March 31, 1911, from Tucson, Arizona, through the kindness of Dr. D. T. MacDougal have yielded a pedigree line which has given me much difficulty in the classification of the rosettes, even under the most favorable environment I could provide, owing to the fact that in this particular strain there is so strong a tendency to precocious development of the stems that the leaf characters even in the climax leaves, are frequently of the relatively undifferentiated juvenile type. It was just in this difficult material that, during several years, two facts impressed me with the probability that there were present in this strain two independent factors corresponding with the *B* factor of the above notation. These facts were (*a*) the occurrence of a relatively small number of *tenuis* (*Ab*) plants in two $F_2$ families (11413, 11414) derived from a cross between the Tucson biotype and a specimen of *B. bp. tenuis* from the eastern United States. No exact count of the *tenuis* rosettes in these $F_2$ families was made, but it was noted that these *tenuis* rosettes were sufficiently distinct from the rest of the family, that their number could probably have been determined with small degree of error. Only desultory attention was being given at that time, however, to rosette characters, owing to seemingly insurmountable difficulties of classification in this biotype, and to my

interest in certain peculiarities of inflorescence and capsule characters, which will be discussed elsewhere. (*b*) The second fact which suggested the probable occurrence of duplication of the *B* factor in this strain was the frequent preponderance of *rhomboidea*-like plants in the pure-bred families. A large portion of the plants which, because of precocious development, did not reach the full typical adult condition, showed, nevertheless, highly developed *rhomboidea* characters, even when no trace of the elongated *A* lobes was discernible. Other plants in the same pure-bred families showed conspicuous elongation of the primary lobes, thus making certain that the *A* factor was present. If two *B* factors were present, namely *B* and *B'*, associated with only one *A* factor, the greater ease with which the *A* character, as compared with the *B* character, was suppressed by unfavorable conditions, would be readily comprehensible.

With this clue to a possible interpretation of the rosette characters in the Tucson strain, especial note was taken of the $F_2$ families from crosses between the same Tucson biotype and *B. Heegeri simplex*, but in every case the number of individuals which fruited with relatively undifferentiated "juvenile" condition of the rosettes was so great that the $F_2$ ratios gave no fully convincing proof of the correctness of the hypothesis. The results of such crosses are given in Table 2.

TABLE 2

*The Composition of the $F_2$ Progenies from a Cross between Bursa bursa-pastoris heteris from Tucson, Arizona, and B. Heegeri simplex, grown at the Station for Experimental Evolution*

| Pedigree Numbers | | | *heteris* *AB* | *rhomboidea* *aB* | *tenuis* *Ab* | *simplex* *ab* | Ratio *B* : *b* |
|---|---|---|---|---|---|---|---|
| $P_1$ | $F_1$ | $F_2$ | | | | | |
| 11505 | | 13202 | 87 | 44 | 16 | 4 | 6.55 : 1 |
| × | 12353 | 13203 | 189 | 66 | 18 | 12 | 8.50 : 1 |
| 11425 | | 13204 | 76 | 59 | 13 | 9 | 6.14 : 1 |
| | | 13205 | 18 | 13 | 7 | 0 | 4.43 : 1 |
| 11505 | | 13206 | 45 | 42 | 4 | 8 | 7.25 : 1 |
| × | 12354 | 13207 | 35 | 18 | 6 | 4 | 5.30 : 1 |
| 11424 | | 13208 | 142 | 122 | 33 | 14 | 5.62 : 1 |
| Totals | ..... | ..... | 592 | 364 | 97 | 51 | 6.46 : 1 |
| *Expected* | ..... | ..... | *771* | *257* | *51* | *17* | *15.00 : 1* |

The results in the several families were quite consistent, but the deviation from the expected 15 : 1 ratio were in all cases very considerable. If it is taken into account, however, that the demonstrated difficulty in genetical studies with this Tucson strain arises

from the *suppression of dominant characters* it will be obvious that these ratios are modifications from a higher ratio (*e. g.*, 15 : 1) rather than from the 3 : 1 ratio to which the empirical results in fact more closely approximate.

A new attempt to test the constitution of the rosette in the shepherd's-purse of Tucson, was made with seeds received from Dr. Forrest Shreve on November 29, 1914. The same care was given to the culture of the families involved in this new experiment as was exercised in those recorded in Table 2. The better greenhouse facilities available at Princeton as compared with those at Cold Spring Harbor, where the previous cultures had been grown, made it possible to secure a closer approximation to the expected ratios, as seen in Table 3, the deviation being the same as before *in direction* but less in amount.

TABLE 3

*The Composition of the $F_2$ Progenies from a Cross between Bursa bursa-pastoris heteris from Tucson, Arizona, and B. Heegeri simplex grown at Princeton University*

| Pedigree Numbers | | | *heteris* *AB* | *rhomboidea* *aB* | *tenuis* *Ab* | *simplex* *ab* | Ratio *B* : *b* |
|---|---|---|---|---|---|---|---|
| $P_1$ | $F_1$ | $F_2$ | | | | | |
| 13241 × 1338 | 14387 | 15423 | 143 | 76 | 11 | 8 | 11.53 : 1 |
| | | 15424 | 14 | 7 | 2 | 1 | 7.00 : 1 |
| Totals | | | 157 | 83 | 13 | 9 | 10.91 : 1 |
| *Expected* | | | *185* | *61* | *12* | *4* | *15.00 : 1* |

Fortunately for genetical studies on the rosette characters of shepherd's-purse, such extensive suppression of characters occurs in nearly all of the other biotypes which have been under observation, only as a result of distinctly unfavorable environmental conditions. The study of a large number of these biotypes from other regions, in crosses with *B. Heegeri simplex*, has brought to light several other cases of probable duplication of the *B* factor, as shown in Table 4.

The cultures in Table 4 also show for the most part distinctly defective ratios, due certainly in the main to the fact that they were being grown in an extensive study of the capsule determiners, and that in consequence suitable conditions were not provided in many cases for full development of the rosette characters. Here and there a ratio closely agrees with the expected $F_2$ ratio, 15 : 1, the best fits being seen in certain families grown from seeds from Bremen, Germany. By chance these families from Bremen grew under more favorable conditions than many of the other cultures listed in this table and this fact doubtless explains in part why they show a closer approxima-

TABLE 4

*The Composition of $F_2$ Progenies from Crosses of Bursa Heegeri simplex and Members of Wild Biotypes of B. bursa-pastoris which Probably Possessed Dimeric B lobes*

| Origin | Pedigree Numbers | | | *heteris AB* | *rhomboidea aB* | *tenuis Ab* | *simplex ab* | Ratio *B* : *b* |
|---|---|---|---|---|---|---|---|---|
| | $P_1$ | $F_1$ | $F_2$ | | | | | |
| Groningen, Holland | 1334 × 13179 | 14354 | 15337 | 112 | 27 | 20 | 2 | 6.32 : 1[3] |
| | | | 15338 | 58 | 20 | 12 | 4 | 4.88 : 1[3] |
| | | | 15339 | 189 | 109 | 14 | 13 | 11.04 : 1 |
| Berlin | 13220 × 1376 | 14367 | 15379 | — | 286 | — | 35 | 8.17 : 1 |
| | | | 15380 | — | 56 | — | 5 | 11.20 : 1 |
| | | | 15381 | 42 | 8 | 4 | 1 | 10.00 : 1 |
| | 13222 × 1376 | 14368 | 15384 | 216 | 86 | 11 | 7 | 16.78 : 1 |
| | 13225 × 13179 | 14372 | 15391 | 60 | 13 | 16 | 20 | 2.03 : 1[3] |
| | | | 15392 | 53 | 16 | 15 | 7 | 3.14 : 1[3] |
| | | | 15393 | 208 | 38 | 8 | 10 | 13.67 : 1 |
| | 13227 × 1376 | 14374 | 15397 | 170 | 26 | 15 | 2 | 11.53 : 1 |
| | | | 15398 | 72 | 25 | 2 | 1 | 32.33 : 1 |
| | 13229 × 13179 | 14377 | 15401 | 116 | 30 | 18 | 7 | 5.84 : 1[3] |
| | | | 15402 | 162 | 5 | 2 | 2 | 41.75 : 1 |
| | | | 15403 | 243 | 74 | 4 | 2 | 52.83 : 1 |
| Bremen | 13231 × 1376 | 14378 | 15404 | 218 | 69 | 14 | 9 | 12.48 : 1 |
| | | | 15405 | 189 | 73 | 13 | 5 | 14.56 : 1 |
| | | | 15406 | 210 | 77 | 15 | 5 | 14.35 : 1 |
| | 13232 × 1376 | 14379 | 15407 | — | 151 | — | 17 | 8.88 : 1 |
| | | | 15408 | — | 103 | — | 12 | 8.58 : 1 |
| | | | 15409 | — | 106 | — | 11 | 9.63 : 1 |
| | | | 15410 | — | 282 | — | 18 | 15.67 : 1 |
| | | | 15411 | — | 167 | — | 12 | 13.92 : 1 |
| | | | 15412 | — | 262 | — | 61 | 4.30 : 1[3] |
| | | | 15413 | — | 198 | — | 23 | 8.61 : 1 |
| | 13237 × 1376 | 14383 | 15415 | — | 202 | — | 27 | 7.48 : 1 |
| | | | 15416 | — | 298 | — | 26 | 11.46 : 1 |
| | | | 15417 | — | 257 | — | 19 | 13.53 : 1 |
| Wales | 1337 × 1338 | 14357 | 15355 | — | 85 | — | 6 | 14.17 : 1 |

[3] These families passed the winter in the open field, and suffered considerable injury. This doubtless accounts for their very great deviation from the 15 : 1 ratio. Small samples from each of these families retained in the greenhouse yielded ratios much nearer to 15 : 1. Only for this reason are these families included here

tion to the expected ratios. In families No. 15405 and 15406, which were given the most careful and detailed study, there was little evidence of the suppression of dominant characters, except that in a few specimens it was a little difficult to be quite sure whether the *A* lobe was present or not and it is not improbable therefore that a few *heteris* plants have been erroneously included in the *rhomboidea* group, but this does not affect the ratios relative to the presence or absence of the *B* factor. On the whole, the three families derived from $F_1$ plants of pedigree 14378, showed the least marked tendency to the suppression of the dominant lobing, and these families show a close approximation to the expected ratio 45 *AB* : 15 *aB* : 3 *Ab* : 1 *ab*. The close agreement with this ratio in these families, indicates not only the duplication of the *B* factor but also the independence of the two *B* factors from the *A* factor.

While 15 : 1 ratios in the $F_2$ give evidence of duplication, it is highly important to carry the analysis forward at least into the $F_3$ generation in order to secure more convincing proof that the *B* factor was really duplicated in the dominant parent of the original cross. Until now the only families beyond the $F_2$ which have been grown from material in which the *B* factor is duplicated, have been derivatives from the earlier Tucson cultures and, as before, these families were grown primarily for the study of the capsules, and only incidental attention was given to the rosettes. The ratios in these families are also defective, therefore, but they give, nevertheless, strong support to the hypothesis that the *B* factor is duplicated in the Tucson plants. These $F_3$ families are brought together in Table 5.

This table has been arranged into the three groups which are expected in the $F_3$ of a cross involving duplication of determiners. In the first section are the families which bred true to the *B* lobing; in the second section are those which split in the ratio 15 : 1, and in the third section are those which split into 3 : 1. The results may be summarized as follows: 19 $F_3$ families contained neither *tenuis* nor *simplex* individuals, seeming to indicate that the 19 parents of these had at least one of the *B* factors homozygous; 3 families showed ratios which may be assumed to represent the 15 : 1 class, showing that the 3 parents of these had both *B* and *B′* present in the hetero-

as probably having a duplication of the *B* lobe. As stated in footnote to Table 1, 15 : 1 and 3 : 1 ratios might both occur in the $F_2$ families grown from plants in a single $F_1$ family, if the wild form used in the cross happened to be heterozygous for one or the other of the *B* factors. Thus

*BBB′b′* × *bbb′b′* = *BbB′b′*, yielding 15 : 1, and *Bbb′b′* yielding 3 : 1.

This situation appears to have been realized in two cases, involving $F_1$ families 14357 from Wales and 14368 from Berlin. These two crosses are included in both Tables 1 and 4.

TABLE 5

*Composition of $F_3$ Families from $F_2$ Parents Having B Lobes in Crosses between B. Heegeri simplex and a Biotype of B. bursa-pastoris heteris from Tucson, Arizona*

| Pedigree Numbers | | *heteris* *AB* | *rhomboidea* *aB* | *tenuis* *Ab* | *simplex* *ab* | Ratio *B* : *b* |
|---|---|---|---|---|---|---|
| $F_2$ | $F_3$ | | | | | |
| 13202 | 14476 | 57 | 53 | — | — | 1 : 0 |
| | 14477 | 49 | 155 | — | — | 1 : 0 |
| | 14479 | 14 | 9 | — | — | 1 : 0 |
| | 14482 | 22 | 155 | — | — | 1 : 0 |
| | 14483 | 30 | 98 | — | — | 1 : 0 |
| | 14487 | 30 | 3 | — | — | 1 : 0 |
| 13203 | 14488 | 24 | 68 | — | — | 1 : 0 |
| | 14489 | 6 | 21 | — | — | 1 : 0 |
| | 14490 | — | 80 | — | 1[4] | 80 : 1 |
| | 14495 | — | 30 | — | — | 1 : 0 |
| | 14496 | — | 245 | — | — | 1 : 0 |
| 13204 | 14499 | 2 | 17 | — | — | 1 : 0 |
| | 14503 | 2 | 74 | — | — | 1 : 0 |
| | 14506 | — | 115 | — | — | 1 : 0 |
| | 14508 | — | 60 | — | — | 1 : 0 |
| | 14509 | 28 | 57 | — | — | 1 : 0 |
| | 14511 | 2 | 44 | — | — | 1 : 0 |
| 13208 | 14513 | 56 | 18 | — | — | 1 : 0 |
| | 14514 | — | 13 | — | — | 1 : 0 |
| 13202 | 14480 | 93 | 216 | 16 | 3 | 16.22 : 1 |
| 13203 | 14492 | 11 | 12 | 1 | — | 23.00 : 1 |
| 13204 | 14512 | 76 | 42 | 5 | 3 | 14.75 : 1 |
| 13202 | 14478 | 58 | 9 | 19 | 3 | 3.05 : 1 |
| | 14484 | — | 125 | — | 82 | 1.52 : 1 |
| | 14485 | 36 | 1 | 18 | — | 2.06 : 1 |
| 13204 | 14500 | 59 | 104 | 12 | 27 | 4.18 : 1 |
| | 14504 | — | 66 | — | 27 | 2.44 : 1 |
| | 14505 | 3 | 60 | — | 24 | 2.62 : 1 |
| | 14510 | 91 | 61 | 36 | — | 4.22 : 1 |

zygous state, *i. e.*, *BbB′b′;* while 7 families gave ratios which may be appropriately referred to the 3 : 1 group, indicating that the parents of these had but one of the *B* factors and this one heterozygous, *e. g.*, *Bbb′b′* or *bbB′b′*. According to theoretical expectation for the number of families given in Table 5 these three groups should occur in the ratio

[4] The occurrence of one *simplex* in this family is of unknown significance. It may represent an unusually defective 15 : 1 ratio, but the deviation is so much greater than in any other family that other possibilities seem more likely to be true. From all my experience with these pedigrees, it seems probable that this "*simplex*" individual is merely a *rhomboidea* modified by the suppression of the *B* lobing. There remain also the possibility of "loss mutation" and of a technical error.

14 : 8 : 8 instead of 19 : 3 : 7. A nearer agreement might well have been expected even with this small number of families. The discrepancy is probably due in part to the small size of some of the families. Thus among the families which were of necessity included in the first section of the table there are six families, the largest of which had no more than 33 individuals and if these families belonged properly to the *second* group of the table, only 1 or 2 individuals of the recessive type were to have been expected. That some of these small families which contained no recessives, had them nevertheless potentially present may be taken as a certainty. Only 5 such families need be shifted from the first section of the table to the second section, to bring about as perfect agreement with the expected ratio as is theoretically possible among 29 $F_3$ families.

A more positive demonstration of the duplication of the *B* factor may be expected from the $F_3$ families derived from the Bremen biotypes in which the suppression of the dominant rosette characters is less extensive. Further experiments involving these biotypes are in progress.

## Discussion

The discovery of a second case of duplication of determiners in *Bursa bursa-pastoris* owes its chief interest to the facts pointed out in one of my former papers (Shull, 1914), (*a*) that cases of actual duplication of genes appears to be rare, and (*b*) that there is some likelihood that the duplication of factors may involve "a series of special genotypic phenomena."

It will be recalled that only in the red pericarp of wheat, yellow endosperm of maize, the occurrence of a ligule in oats, and of triangular capsules in shepherd's-purse, was the demonstration of dimery considered adequate. Several new instances have been brought to light more recently, and at least one of these must be admitted as fully demonstrated (Ikeno, 1917). This relates to the quantity and distribution of chlorophyll in *Plantago major*, in which two seemingly identical factors, *G* and *H*, determine independently the normal full green pigmentation of the plant. Either of these two factors may be entirely wanting, without modifying in any way the self-green color, but when both are absent, the plants are conspicuously variegated with white or pale yellowish blotches and stripes, the total quantity of chlorophyll being considerably reduced.

Hallqvist (1916) has found the pinnatifid leaves of *Brassica Napus* apparently produced independently by two factors, the recessive undivided type reappearing in the $F_2$ in only one plant in 16. As the lobed plants showed considerable variation the results in $F_3$ will be necessary to confirm the author's conclusion in this case.

Of cases in which two or more factors do not produce visibly *identical* but only more or less *similar* results as in the black glume color in oats (Nilsson-Ehle, 1908, 1909), there are many more instances. These do not represent instances of duplication at all, of course, though they may be expected to grade into cases which would be indistinguishable from duplication. Several of the eye-color and body-color factors of *Drosophila* appear to be of this nature, and some real duplication may also be present in this group. Some of these *Drosophila* characters should have been included in my former paper, but they had not been to my knowledge cited as examples of "multiple" factors. They have since been so treated, and with obvious propriety, by Morgan, Sturtevant, Muller and Bridges (1915). The characters specifically mentioned by these authors are (*a*) pink eye-color which is determined independently by factors associated respectively, one with the sex (or X) chromosome, and the other with the "third" chromosome; and (*b*) dark body-color, which is independently produced by two genes which have been designated "black" and "ebony," one in the "second" and the other in the "third" chromosome. Black and ebony are not identical but merely so similar that their separation is not practicable when associated in the same family.

Howard and Howard (1912, 1915) have shown that velvet chaff of wheat is independently produced by two factors, *L* and *S*, but here also the factors are clearly not duplicates of each other, for *S* produces short hairs and *L* long silky hairs, while plants containing both factors have a mixture of both types of hairs on the glumes. The same authors have found the long awns of "bearded" wheat to result from the combined action of two factors *B* and *T*, each of which produces short awns in the absence of the other, but *T* produces shorter awns than *B* and the *T* awns are most conspicuous in the distal part of the spike while the *B* awns are more evenly distributed on the spike. In this case the action of both *B* and *T* is cumulative, the fully awned form appearing only when both *B* and *T* are homozygous, *i. e.*, *BBTT*.

An exceedingly interesting case of duplication, should it stand the test of further analysis, is reported by Gates (1915) in a cross between *Oenothera rubricalyx* and *Oe. grandiflora;* for, starting with a heterozygous type supposedly monomeric with respect to the characteristic red pigmentation of the *rubricalyx* bud, he secured in the $F_2$ two 15 : 1 ratios and two 3 : 1 ratios, in addition to one 4 : 1 and four 5 : 1 ratios. In the $F_3$ he records 4 families with a 2 : 1 ratio, one 3 : 1, two 4 : 1, four 15 : 1, and six pure *rubricalyx* (*i. e.*, 1 : 0), besides three families in which the pigmentation of all individuals was intermediate. Gates interprets the several 15 : 1 ratios as evidence that the *R* factor has become duplicated, but owing to the

notorious inharmonies between the inheritance ratios in the Oenotheras and the expectation based on the usual Mendelian methods of segregation and recombination, one may well suspend judgment regarding this case as an instance of duplication, until it has been shown by further analysis of one of these 15 : 1 ratios, that the *rubricalyx* individuals will yield three kinds of families, characterized respectively by the ratios 1 : 0, 15 : 1, and 3 : 1, and that these three kinds of families are produced in approximately the ratio 7 : 4 : 4. Unless this should be the result of the further study, the 15 : 1 ratio noted in several of the $F_2$ and $F_3$ families must have been brought about by some combination of circumstances, other than the typical Mendelian distribution of two duplicate factors for the *rubricalyx* pigmentation.

Gates discusses at some length two of the several methods by which one may reasonably suppose duplication of factors to come about. He seems to imply (Gates, 1915, p. 204) that my discussion of this subject does not adequately cover the several possibilities. He then proceeds to present two of the same possibilities as if they were original propositions of his own. These several possibilities are (*a*) the occurrence of independent mutations affecting in the same or closely similar manner non-homologous chromosomes; (*b*) the mating of non-homologous chromosomes; and (*c*) the transposition of parts of chromosomes by what I have called a "sort of longitudinal crossing-over" (Shull, 1914, p. 139). Only the first two of these propositions are considered by Gates and he agrees with me that both of the processes (*a*) and (*b*) have probably actually resulted in the duplication of factors. He thinks that repeated mutations were responsible for the duplication of red pericarp color in Nilsson-Ehle's wheats, and that mismating of chromosomes will explain the duplication which he believes to have taken place in his *Oenothera rubricalyx* crosses.

Upon unpublished evidence Bridges (1917, p. 454) refers to two cases of duplication in *Drosophila* which seem to result from essentially the longitudinal rearrangement of genotypic materials that I had in mind when suggesting the possibility of "longitudinal crossing-over," though the details of the process as understood by him are somewhat different. He states that a section from the mid-region of one X chromosome appears to have been removed from its accustomed place or locus in that chromosome, and to have become attached to the end of the other X chromosome, its mate. The full account of this case will be awaited with interest.

Accepting the validity of these several methods of duplication, one may well ask in each specific case whether circumstances make possible a judgment as to which method was probably responsible for the duplication in question. I have assumed that the complexity

of the structure of the triangular capsule of *Bursa bursa-pastoris* as compared with the *Heegeri* type of capsule, is strong evidence against the duplication of the factor for this complex character through independently repeated mutations affecting different chromosome pairs (Shull, 1914, p. 141). The character under consideration in the present paper, namely the *B* lobing of the rosette leaves, appears to justify the same observation. The production of leaves divided at frequent intervals by sinuses reaching to the midrib, and bearing characteristic secondary lobes and sinuses, involves the control of the number and direction of cell divisions through very long and complexly branched cell lineages, and it is scarcely conceivable that such specific control of these long cell lineages should be exactly duplicated by independent mutations affecting different chromosomes.

It appears to me much more logical to assume that such a rearrangement of the genotype has taken place that the two *B* determiners which are allelomorphic to each other in the homozygous monomeric strains, assumed new positions, whereby they became associated with chromosomes belonging to different pairs, and thus capable of inclusion in the same germ cell.

As these two factors, *B* and *B'*, are apparently entirely independent of each other, it may be taken for granted that they are associated with different chromosome pairs. They could become thus associated by either of the two methods, (*b*) or (*c*), but in the absence of known linkage relations, there is nothing to indicate which of these two methods has been the more probably responsible for the duplication of the *B* factor,—whether a rearrangement of whole chromosomes or the rearrangement of parts of chromosomes through a so-called "longitudinal crossing-over."

All these suggestions as to the origin of duplicate determiners assume the duplication to be a derivative condition; but it may also be in some cases the primitive condition from which monomeric and recessive strains may have arisen as a result of repeated "loss" mutations, as stated in my previous paper (1914, p. 137). Studies of the geographical distribution of the duplicated factors may throw some light upon the relative age of the monomeric and polymeric types, for if wild biotypes almost universally possess the duplicated factors, it may be assumed that this condition is either primitive or at least relatively old, while a much restricted and more or less definitely circumscribed range may be accepted as a criterion of relatively recent origin from the monomeric condition.

In regard to the *B* leaf-lobe factor it will be noted by reference to the tables, that plants showing the duplication (Table 4) have been found at Tucson, Arizona, at Cardiff, Wales, at Groningen, Holland,

at Bremen and Berlin, Germany, and perhaps at Peking, China, while monomeric *B* lobes (Table 1) have been demonstrated in strains from all these places except Tucson, Arizona. Besides these places in which the two types have been found associated together, the monomeric condition has been found at Chicago, Illinois, at New Carlisle, Ohio, at Landau, Germany, and probably at Vicenza, Italy, in which places duplicated factors for this character have not yet been discovered. Excepting only Landau, Germany, these localities in which duplication of the *B* factor has not yet been found, have been represented in my cultures by only one wild *B*-lobed plant from each locality. It may be merely a matter of chance that the first plant from each of these localities had but one of the *B* factors. It should also be noted that from the only region in which *monomeric B* lobes have not been found, namely at Tucson, Arizona, only two wild plants have yet been tested, a number quite too small to give any confidence in the suggested inference that no biotypes with monomeric *B* lobes occur at that place. It is obviously necessary to make the study of geographical distribution of these *B* factors much more extensive before safe conclusions may be drawn as to the primitive or derivative condition of the *B* lobe with respect to duplication. This is a work in which many students might lend assistance by crossing together the several wild biotypes from their own localities.

## Summary

The leaf lobes of shepherd's-purse are controlled by Mendelian factors *A*, producing elongated sharp lobes, and *B* which divides the leaf to the midrib and brings to light certain characteristic secondary lobing. The action of these factors is easily suppressed or obscured by unfavorable environmental conditions, and the inheritance ratios are usually more or less defective on this account. In previous papers both of these characters have been reported to be monomeric, *i. e.*, each was found to be controlled by a single factor.

It is shown in the present paper that two factors, *B* and *B'*, exist in certain strains and that these two factors produce the same characteristic lobing of the leaves, but are inherited independently of each other and of the factor *A*.

The biotypes having the *B* factor duplicated appear to be less widely distributed than those which are monomeric with respect to the *B* lobes. More extensive data are needed on this point, but if the present indications are confirmed, the relatively less frequency of the dimeric condition is taken to mean that the duplication of this factor has taken place at a relatively recent date.

The morphological complexity of the character produced by the *B* and *B′* factors is believed to indicate that duplication has come about through a physical rearrangement in the genotype rather than by a repeated mutation affecting in like manner chromosomes belonging to distinct pairs.

My acknowledgments and thanks are due to the following correspondents, to whom I am indebted for seeds of the wild biotypes which were used in the present study: D. T. MacDougal, F. Shreve, J. M. Shull, C. A. Shull, A. H. Trow, Tine Tammes, G. Bitter, E. Baur, L. Gross, G. Molon, and T. Z. Chang.

## LITERATURE CITED

**Bridges, C. B.** Deficiency. Genetics 2: 445–465. 1917.

**Gates, R. R.** On Successive Duplicate Mutations. Biol. Bull. 29: 204–220. 1915.

**Hallqvist, Carl** Ein neuer Fall von Dimerie bei Brassica Napus. Bot. Not. 1: 39–42. 1916.

**Howard, A., and Howard, Gabrielle L. C.** On the Inheritance of Some Characters in Wheat I. Mem. Dept. Agr. India 5: No. 1. 1912.

—— On the Inheritance of Some Characters in Wheat II. Mem. Dept. Agr. India 7: 273–285. 1915.

**Ikeno, S.** Variegation in Plantago. Genetics 2: 390–416. 1917.

**Morgan, T. H., Sturtevant, A. H., Muller, H. J., and Bridges, C. B.** The Mechanism of Mendelian Heredity. Pp. xiii + 262. New York: Henry Holt & Co. 1915.

**Nilsson-Ehle, H.** Einige Ergebnisse von Kreuzungen bei Hafer und Weizen. Botaniska Notiser, pp. 257–294. 1908.

—— Kreuzungsuntersuchungen an Hafer und Weizen. Lunds Universitets Årsskrift, N. F. Afd. 2, Bd. 5, Nr. 2, pp. 122. 1909.

**Shull, G. H.** Results of Crossing Bursa bursa-pastoris and Bursa Heegeri. Proc. 7th Internat. Cong. Zoöl. 1907, Boston 1912. "Advance reprint" in 1910, 6 pp. 1907.

—— Bursa bursa-pastoris and Bursa Heegeri: Biotypes and Hybrids. Carnegie Institution of Washington. Publ. No. 112, pp. 57. 1909.

—— Defective Inheritance-ratios in Bursa hybrids. Verh. d. naturf. Verein Brünn 49: 157–168. 1911.

—— Duplicate genes for capsule-form in Bursa bursa-pastoris. Zeitschr. f. ind. Abstamm.- u. Vererb. 12: 97–149. 1914.

# ISOLATION AND SPECIFIC CHANGE

EDMUND W. SINNOTT

*Connecticut Agricultural College*

Those regions of the earth which are so isolated biologically that the dispersal of plants or animals between them and other areas is difficult or impossible are characterized, as is well known, by large numbers of species and genera which are peculiar to them or are "endemic." In general, the more definitely isolated the region the higher is its proportion of local forms. Why isolation should be associated so universally with the presence of these endemic types is a problem which has excited speculation. It is evident that once a local race is established, isolation will operate effectively to maintain it, both by preventing its dispersal abroad and by excluding invaders which might supplant it. The difficult problem has been to account for the actual origin of the endemic types themselves in the first place. In an attempt to throw light on this problem a study has been made of the floras of a number of islands which are isolated to a greater or less degree from adjacent land masses and have developed a large body of local species and genera of vascular plants.[1]

Certain elements of the endemic flora in all these islands are doubtless not of local origin but are "relicts," remnants of types once much more widely spread, which owe their preservation to freedom from the keener competition of the mainland. These types do not concern our problem. As to just how abundant they are we do not know, but those forms which stand well apart and have no near relatives in the islands or elsewhere are probably to be looked upon as relicts. From the close similarity of most of the endemic species and genera with others on near-by islands or on the adjacent mainland, however, and from their frequent occurrence as groups of related forms, it is evident that the bulk of the endemic element in these floras is actually of local origin.

Several hypotheses have been put forward to account for the origin of these endemic forms. Some investigators have pointed to natural selection as the primary factor, believing that new types are produced by this agency to fit exactly the peculiar conditions in each region, rather than a wide environmental range. Others, less con-

[1] These islands are New Zealand, Ceylon, Hawaii, the Galapagos, Juan Fernandez, St. Helena, Sokotra and Mauritius.

vinced of the efficacy of selection, believe that each region has its own characteristic environmental complex, different from that of all others, which modifies directly the germ plasm of the animal and plant types living under it and stamps upon them their local distinctions. Both of these views regard the environment as the most important factor in specific change and look upon isolation as the agency which, through providing a comparatively simple and constant environment, allows a much closer adjustment to it by the plant and animal population than is possible on wider areas, and hence leads to the production of large numbers of local species. Still another view considers that most, if not all, of these endemic and peculiar forms would have developed anyway under the progressive evolution of their type, and owe their local character not to a dependence, direct or indirect, upon a specific environment, but merely to the fact that they have been unable to become dispersed abroad.

An analysis of the insular floras under investigation presents certain facts which have a bearing on the problem. It makes evident, in the first place, that endemism is by no means uniformly characteristic of all the elements in the flora but that it occurs very much more frequently in certain of the great groups of vascular plants than in others. The vascular cryptogams, for example, which comprise an important part of the vegetation of these islands, include but few species or genera which are confined to any one island or island group. The glumaceous monocotyledons—Gramineae, Cyperaceae and Juncaceae—which are also abundant, are represented infrequently among the endemic forms, though they are somewhat commoner there than are the vascular cryptogams. It is in the petaloideous monocotyledons and the dicotyledons that the great bulk of the endemics occurs throughout all of these insular floras. Not only hosts of the species but almost all of the local genera belong to these groups. Certain families, like the Orchidaceae and the Compositae, often contain almost nothing but endemic species. How great is this disparity in the extent to which endemism occurs is evident from the following table, which is an average of the eight island groups investigated.

| | Species | | Genera | |
|---|---|---|---|---|
| | Endemic | Non-endemic | Endemic | Non-endemic |
| Vascular Cryptogams | 23.2% | 76.8% | 1.9% | 98.1% |
| Glumaceous Monocotyledons | 31.4% | 68.6% | 2.2% | 97.8% |
| Petaloideous Monocotyledons | 59.0% | 41.0% | 9.7% | 91.3% |
| Dicotyledons | 61.7% | 38.3% | 11.4% | 88.6% |

What bearing have these facts on our problem of the origin of local types? They offer little support, in the first place, to the theory

that natural selection has presided over the appearance of these new forms, for groups which have developed few or no endemic species are apparently as successful elements of the vegetation as are those in which such species have been abundantly produced. In fact, Willis[2] has gathered evidence from the flora of Ceylon which seems to show that the non-endemic species are more successful, as a whole, than the endemic ones, a fact which militates strongly against the theory of selection. Of course we are confronted here, also, with one of the major difficulties urged against natural selection, namely that it can never create but can only eliminate.

Nor do our figures support the theory that local forms owe their origin to the direct action of the environment, for such a theory cannot well explain the abundance of endemic species in some groups and their rarity in others. It may be argued that the vascular cryptogams and glumaceous monocotyledons are more primitive and slow-changing types than the petaliferous groups, and are thus able longer to resist the pressure of the environment and to maintain their original characters. We have little evidence, however, that this is actually the case. Ferns under cultivation seem to be very plastic, and our knowledge of the genetics of the Gramineae, at least, does not indicate that they are a particularly rigid group.

Both of these views look to the environment as the factor, either direct or indirect, which is chiefly responsible for the origin of new forms, and both are open to the objection (among others) that although the whole flora is subject to the same environment, these new forms develop only in certain groups. Our third alternative largely disregards the environment. It looks upon the actual production of new types as due to factors within the organism rather than in its surroundings, and considers that the locally developed species and genera in the floras under discussion would have appeared in these regions whether isolation existed or not. Isolation is thus regarded merely as the agency which keeps these new forms local and endemic by preventing their dispersal beyond the place of their birth. Of course such a theory allows for the play of selection in weeding out all new forms which were distinctly unsuited to the environment under which they appeared.

But is not this view also open to the objection which we have offered to the others, that it cannot account for the rarity of endemism in certain groups and its extreme commonness in others? A study of the methods of reproduction in plants belonging to these two categories suggests an answer to this question. Vascular cryptogams in the great majority of cases have bisexual gametophytes and are

[2] Willis, J. C., The evolution of species in Ceylon, with reference to the dying out of species. Annals of Botany 30: 1–23. 1916.

doubtless almost invariably self-fertilized. In the glumaceous monocotyledons, although crossing is certainly not uncommon, it will probably be agreed that self-fertilization is also the general rule. In these two groups we have noted that local species and genera are very rare. In the petaloideous monocotyledons and in the great majority of dicotyledons, on the other hand, the flowers are attractive to insects and cross-fertilization preponderates. As far as our knowledge goes, there are few petaliferous species which are not at least occasionally cross-pollinated. These facts are significant when we remember that it is among such forms that local types are produced in great abundance. In short, our analyses of these insular floras supports strongly the theory recently emphasized by Lotsy and others that hybridization is the most important factor in the production of new forms; self-fertilized types changing slowly, cross-fertilized ones, rapidly. The unequal development of endemism in certain floral elements, therefore, which neither the theory of selection or that of the direct effect of the environment can well explain, is thus understandable as the result of differences in methods of reproduction, and is quite consistent with the theory that the production of new forms is due primarily to internal causes.

The evidence brought forward by our study of isolated insular floras therefore seems to indicate that isolation is not a factor in evolution but simply in distribution; that it cannot create an endemic *species* but can merely keep a species *endemic*.

## Summary

1. Isolated regions are characterized by possessing large numbers of local, or endemic, species and genera.

2. In the insular floras investigated, endemism is not equally distributed among all plant groups, the local species and genera being rare among vascular cryptogams and glumaceous monocotyledons but very common among petaloideous monocotyledons and dicotyledons.

3. This fact seems to indicate that the environment, whether acting directly or by means of natural selection, has not been the determining factor in the development of endemic forms.

4. Those groups which are poor in endemics are predominantly self-fertilized, those which are rich in endemics, predominantly cross-fertilized; suggesting that hybridization has been the most potent factor in the development of these new forms.

5. Isolation is therefore regarded not as the factor which, by providing a simple, limited and peculiar environment, is responsible for the origin of locally developed species and genera; but merely as the factor which, by prohibiting dispersal, maintains the endemic character of local types which owe their origin to other causes.

# THE RELATIONS OF CROWN-GALL TO OTHER OVERGROWTHS IN PLANTS

ERWIN F. SMITH

*Bureau of Plant Industry, U. S. Department of Agriculture*

In the time assigned the most I can hope to do is to give the barest outline of the suggested relationships. Some of these are well determined; others are only suspected and are mentioned here as hopeful lines of research rather than as definite conclusions. Indeed, I am quite willing to admit that our work on crown gall has opened up more problems than it has settled, but, one way or another, all of this present uncertainty will make for progress and an eventual better understanding of the whole mechanism of overgrowth. My own belief is that all overgrowths are correlated phenomena, are the response of the organism to essentially similar (but not necessarily identical) stimuli, the visible difference in response when brought about by parasites being due to number and location of the parasites, age and kind of tissues invaded, and volume, direction, and velocity of the stimulus exerted. In other words, in every case, I think the stimulus is primarily a physical stimulus due to changed osmotic pressures rather than a direct chemical stimulus. Overgrowths, therefore, do not always involve the presence of a parasite although as observed in nature parasites are probably responsible for most of them.

I. Factors governing type of overgrowth in crown gall.

*A. The host reaction depends on the type of tissue infected.*

(1) *Vascular vs. parenchymatic.* For example, depending on the tissue in which it originates the vessels in a tumor may be numerous or few, the parenchyma abundant or scanty.

(2) *Nexus of cells stimulated, i. e.*, unipotent, multipotent, or totipotent cells. Thus, according to the tissues infected by the crown gall schizomycete, we have it causing either organoid galls or histioid galls.

(3) *Rate of growth.* The rate of growth depends on the readily available supply of food and water, on the age of the tissues when infected and on the species

attacked—some species are not subject to this disease; old tissues respond slowly.

(4) *Individual differences.* There are, I believe, individual differences in susceptibility as well as species differences.

*B. The host reaction depends also on the activities of the parasite (Bact. tumefaciens) which are variable.*

(1) *Loss of virulence on culture media.* The cause of virulence is not known. The effect of long continued growth on culture media is to reduce the virulence of the organism and finally to destroy it altogether.

(*a*) *"Old" vs. "resistant" cultures of Paris daisy organism.* Our first isolation from Paris daisy was extremely virulent in the beginning but lost all power to produce galls in about three years. Another isolation which we called "Resistant Daisy" is now slowly losing virulence at the end of three and one half years.

(*b*) *New vs. old cultures of poplar isolation.* An isolation from a poplar tumor was extremely virulent for some time (several years) but has now lost all power to produce tumors. Along with this loss has come a progressive thickening and toughening of the pellicle on bouillon. This was true also of the daisy isolation which lost its virulence.

Apparently this loss of virulence is not correlated with loss of power to produce formic acid for, according to the chemist, the non-virulent poplar organism still produces that substance. Loss of power to infect must be related, however, to loss of some chemical or physical property once possessed, and surely we ought to be able to discover the exact nature of this loss. Some strains of *Bact. tumefaciens* lose virulence much sooner than others. One of our strains (from hop) is still virulent after nine years on culture media.[1]

(2) *Not every isolation is a distinct strain.* I speak of "strains" only when I know that cultural

[1] Ten years, as this now goes through the press.

and other differences exist; otherwise, I speak only of "isolations." There are certainly two of these crown gall strains, and probably many.

(3) *Feeble and virulent strains exist in nature, i. e., there is variation in virulence of colonies from the same source—hop, carnation, rose, sugar beet, etc.* The author believes that the crown gall bacteria not only lose virulence on culture media but also in the tissue of the gall. Examples are: (*a*) of three colonies selected as typical from plates poured from a hop tumor in 1910 only one proved infectious; (*b*) of six colonies plated from a witch broom on carnation, all of which looked alike and typical for crown gall, only one was found to be able to cause tumors when inoculated; (*c*) of seven colonies selected as typical from a plate poured from a rose gall only three proved infectious, and of these two were actively infectious, while the other was only feebly so; (*d*) of five colonies selected as typical from a plate poured from a tumor on *Pelargonium* none proved infectious, although in advance we felt quite sure of all of these colonies; (*e*) of thirty colonies selected from plates poured from natural tumors on sugar beets only five were infectious and all feebly so (Bul. 213, pp. 192–194 and Plate XXXVI).

The first and natural supposition when a culture has lost virulence is that some intruder has displaced the right organism; and when only certain colonies on a plate are infectious, that the others are intruders however much they may resemble the right organism. I cannot say that we have absolutely excluded this hypothesis, to which I held strongly in the beginning, but we are gradually coming to believe that it does not explain all the facts.

II. Some other types of plant galls.

(1) *Nonparasitic intumescences.* These can be produced in several ways: by overwatering and exposure to

excessively moist air; by exposure to very dilute vapors of ammonia or of formaldehyd; by application of a great variety of soluble substances not the products of parasites, *e. g.*, copper salts; by painting the surface with vaseline and other insoluble substances which interfere with the gas exchange; by freezing lightly (Harvey), etc.

(2) *Non-cancerous bacterial tumors*—olive knot (due to *Bact. savastanoi*), beet tumor (due to *Bact. beticola*). In these the bacteria are abundant and easily seen occupying the vascular bundles and the spaces between cells. Bacterial cavities are produced and the overgrowths are only superficially like crown galls. The secondary tumors are not developed from tumor strands. When the bacteria are intracellular the cells are destroyed.

(3) *Nematode galls.* In galls due to *Heterodera radicicola* giant cells, *i. e.*, several to many nucleate cells, are common. Parasitic nematodes which do not produce galls. Here the anal excretions are voided outside of the plant (Cobb). Occurrence of several-nucleate cells in crown gall.

(4) *Various fungous galls.* Parenchymatic *vs.* woody; perishable *vs.* persistent; witch brooms (see newer work on crown gall). Parenchyma strands (Dodge).

(5) *Insect galls which show features resembling crown galls.*

(*a*) Galls bearing leaves; galls bearing roots; galls bearing modified trichomes. We have now succeeded in producing on internodes by bacterial inoculation crown galls bearing roots, leafy shoots, flower buds, and modified trichomes.

(*b*) Galls with cortex carrying bright colors—purple, red, yellow. Crown galls produced on pale green balsam stems show a red color in their cortex provided the plants bear colored flowers, but not if they bear white flowers. The production of red pigment in the cortex has been seen also in axillary (teratoid) crown galls developed on red-flowered Pelargoniums. Etiolation. Excess of chlorophyll.

(*c*) Galls opening by opercula—strange but not more so than twin-leaf fruits opening in a similar manner, or than a double vascular cylinder in *Ricinus* with death of intermediate pith and separation into two cylinders. (Jour. Ag. Res. Jan. 29, '17, pl. 37).

(*d*) Galls with very definite and distinct strata of gall tissue—parenchymatic, vascular and protective, *e. g.*, cynipid galls. Küster's prosoplasmatic galls.

Many insect galls differ from crown galls in that (1) the parasites are few or reduced to a single organism, and (2) are *extracellular*, whereas in crown gall the parasites are more numerous and are *intracellular*. Many differences in structure, even of the more complex galls, can be explained, I think, by these two differences, especially if we assume (3) that the kind of reaction depends on the volume, direction, and velocity of the stimulus, its constant or intermittent flow, and on location, distance, and mobility or immobility of the source of the stimulus. As in various insect galls so in crown galls, there is a tendency toward the production of more primitive tissues and of various anomalously formed organs.

III. *Crown galls are formed by extrusion of chemical substances.* I have recently produced galls with diluted crown-gall products and this, it seems to me, suggests a new method of attacking gall problems in general, especially those in which the gall parasites can be cultivated pure in sufficient quantity for chemical analysis, *e. g.*, various fungi. Striking results have been obtained but many tests are yet to be made with the crown-gall substances in various dilutions, mixed and separate on a variety of tissues of responsive ages. Various types of cell growths have been produced by the action of ammonia, acetic acid, formic acid, aldehyd, etc. (all products of *Bacterium tumefaciens*, the crown-gall organism) in less than killing doses, that is, various degrees of hypertrophy and hyperplasia of cells and mixtures of the two have been observed. Sometimes there is great stretching of cells as in certain fungous and insect galls. Giant cells in the animal pathologist's sense of that word, namely, cells containing several to many nuclei, such as occur in the common nematode galls, are to be searched for in all sorts of plant galls and to be produced, if possible, experimentally, *i. e.*, with gall-forming substances. In due time we shall be able, I believe, to get these multinucleate cells at will. Probably they are weakened cells. Two very important things to be determined are whether the size of the cell depends on the volume or rate of movement of the stimulus or on the kind of stimulus, and whether mixed stimuli applied in varying proportions change the manner of cell reaction.

IV. *Other effects of parasitic excretions.* I believe also from what I have seen and have obtained to some extent by experiment that thyloses, fasciations, distortions of tissues, and various duplications, simplifications and inverse tissue differentiations are caused by the excretions of feeble parasites although in nature probably all are not so caused.

Finally, I would suggest that the application of chemical substances in various dilutions to growing plants or plant organs, such substances in particular as are known or suspected to be produced by living organisms, or are present in soils as a result of decompositions, may prove to be a hopeful way of attacking certain unsolved and difficult problems in plant pathology, *e. g.*, the aetiology of the mosaic diseases, the cause of various growth limitations, etc.

## Literature

Those who wish details on crown gall are referred to the following papers:

For the older work: Science, N. S., April 26, 1907; Phytopathology, Vol. I, No. 1, Feb., 1911; Science, N. S., February 2, 1912; 1$^{er}$ Congrès International de Pathologie Comparée, Tome II, Paris, 1912; 17th International Congress of Medicine, London, 1913, Section III, General Pathology; and Bulletins 213 and 255, Bureau of Plant Industry, to be had from the Superintendent of Documents, Government Printing Office, price 40 and 50 cents, respectively.

For the newer work so far as published: The Journal of Agricultural Research, April 24, 1916; The Journal of Cancer Research, April, 1916; Science, N. S., June 23, 1916; The Journal of Agricultural Research, January 29, 1917; Bulletin of the Johns Hopkins Hospital, Sept., 1917; and Proceedings of the American Philosophical Society, Vol. 56, 1917.

Separates of most of these papers may be had from the writer.

# CONTACT STIMULATION

GEORGE E. STONE

*Amherst, Massachusetts*

The experiments presented here have been carried on since 1904, at which time the writer observed some rather remarkable stimulated growth responses induced in sunflowers when surrounded by wire netting. At the time these observations were made we were carrying on investigations relative to the effect of varying atmospheric electrical potentials on plant growth, and for this purpose we made use of sunflowers established in large earthen pots or wooden boxes located at different elevations in the open air. In some of these experiments the plants were surrounded with wire netting and in contact with the same but not with the soil, while in others (normals) no wire netting was used. In some instances the wire netting was not only in contact with the plants, but with the soil in which the plants were growing; the soil being grounded by the use of copper plates in the bottom of the boxes and by insulated wire, which led to the earth. In other instances the plants were in contact with wire netting and the soil, but were not grounded. The problem under consideration at that time, however, more particularly concerned itself with the influences of atmospheric electricity on plant growth, for which purpose organisms of various kinds, including bacteria, were exposed to elevations varying from thirty to sixty feet. Some of the earlier experimenters have maintained that when plants were grown in the free atmosphere surrounded with wires, they failed to develop, and would eventually die in consequence of being deprived of the beneficial effects supposed to be derived from atmospheric electricity. In passing we may state that we have never observed any remarkable mortality among plants in consequence of their being surrounded with wires even when the experiments were performed at more or less high elevation above the ground, and under ideal conditions for determining the effects of atmospheric electricity on vegetation. Moreover the growing of plants in conservatories where the electrical conditions of the atmosphere are quite different from those out-of-doors demonstrates the fallacy of this idea. On the other hand, we found that plants were greatly stimulated by wire enclosures, especially when they came in contact with the plants, and also the same stimulation was noted when plants were grown thickly together and the leaves

touched those of other plants. An electrically charged atmosphere, however, exerts a marked stimulation on plants and it is possible to modify the function of organisms located at more or less high elevations by the use of metal coverings. The old idea that milk sours more rapidly during thunder storms, and that plant growth is greater following electrical storms has in reality a fundamental basis. The discovery of contact stimulation led us to modify our methods of studying the effect of electrical potential on plants since we found that when the plants were not in contact with one another, or with the surrounding wire mesh quite different results were obtained. The observations and results obtained by contact of plants with one another and with wires, etc., was so significant that we undertook the investigation of this phase of the problem at that time, and have devoted considerable attention to it since. Some of our earlier experiments were conducted out-of-doors and parallel experiments were carried on in a conservatory. Repeated tests of the air in our conservatory with a water-drip apparatus and electrometer have invariably shown that under ordinary weather conditions there exists no atmospheric electricity in conservatories, the glass apparently acting as a screen. The nature of the stimulation due to contact is probably in no way associated with atmospheric electrical phenomena, or at any rate, the growth responses do not appear to be identical with those resulting from ordinary electrical stimulation. The response to contact is induced by the use of various materials, such as wire, twine, wood and metal stakes, excelsior, sphagnum moss, soil particles or even by the plants being in contact with one another. The same reactions are produced whether the different contact materials used are suspended and only touch the leaves of the plant, or whether they touch both the leaves and soil in which the plants are growing. While there is no evidence to show that these reactions are associated with any changes in the electrical tension of the atmosphere, surrounding the plants, they may, however, be connected with electrical phenomenon. The reactions resulting from contact stimulations are not unlikely quite primitive and universal to plants and probably common to the lower forms of life in general. Probably all organs will prove to be sensitive to contact but from our observation the leaves appear to be especially so. The nature of the reactions appear to be fundamentally similar to those of touch, from which it would seem the more highly differentiated reactions of tendrils and wound responses, etc., originated.

FIG. 1. Showing growth of sunflowers surrounded by wire netting. Note difference in size of plants which have penetrated through the wire-mesh enclosure, a feature of common occurrence.

## METHODS

In the study of the effects of contact of various materials with plants we employed several methods and the experiments were carried on under different conditions. With the exception of some of the earlier experiments which were made out-of-doors, most of them were

conducted in a conservatory where the heat, light and soil conditions were uniform and normal. Some of the experiments were carried on in direct sunlight; others in darkness, while others again were conducted under bell glasses where it was possible to maintain uniform atmospheric moisture and transpiration conditions. Contacts with wire were made with a two-inch-mesh galvanized iron wire netting, and in some cases a one-inch-mesh wire was employed. These were made up into cylinders 4 to 6 feet high and varied in diameter from 8 to 26 inches, according to the size and number of plants employed. These wire cylinders were placed around the plants. In some instances the plants were grown between trellises made of wire netting placed from 6–10 inches apart, in which case the tips or free end of the leaves of the plants came in contact with the wire on two sides. Wooden stakes (dowels) and iron posts driven into the soil were also employed as contact material, the dowels being used in some instances to support loose twine which surrounded the plants and in other cases they were used alone in various combinations. Fishnet made of twine with a mesh of about two inches was employed in a similar manner to that of the wire cylinders, and in some cases the plants were more or less loosely tied up with twine. In the study of the effects of contact on the stems and roots of seedlings, excelsior was employed either loosely in long strands, or cut up more or less in fine shreds as the nature of the experiment required. In the root, contact experiments were made with soil particles which ranged from 16 mm.–0.1 mm. in size, the various grades of material being obtained by sifting through sieves and bolting cloth. The particles were repeatedly washed and sterilized and submerged in jars of water, the latter being previously boiled to exclude air, inasmuch as the presence of air would greatly modify the growth of the seedlings (1).

### Effects of Contact of Plants with One Another

When plants are grown close together, as is the case of some crops, they often come in contact with one another and even in nature contact stimulation plays an important rôle, particularly where certain organisms grow so close to one another that they touch. The growth of some coniferous trees is often such that they are much congested, and in nurseries where many thousands of coniferous seedlings and other nursery plants are grown close together a contact stimulation may sometimes occur. We have, however, no authentic data based upon experiments regarding the behavior of coniferous and other seedlings grown under nursery conditions. Neither have we attempted to differentiate growth which may be due to contact in thick stands of forest growth from those originating from other causes, but some

gardeners and foresters have intimated that they have observed indications of an accelerated growth in height as a result of coniferous seedlings coming in contact with one another. The stimulation effect of contact, however, can be observed in the growth of crops and the

FIG. 2. Showing growth of tomatoes *in situ* in contact and not in contact with one another.

method of close growing of certain economic plants has its advantages. The configuration of plants, however, is greatly modified by close growing, as may be observed in the handling of single-stemmed chrysanthemums by florists, the growth of corn and various other

TABLE 1

*Showing Growth of Tomatoes (Lycopersicum esculentum Mill.) in Contact and Not in Contact with One Another*[1]

| | Average Height and Diameter of Plants (Centimeters) | | | |
|---|---|---|---|---|
| | Height | Diameter | Percentage Gain by Contact | |
| | | | Height | Diameter |
| Normal | 19.41 | .46 | | |
| Contact | 31.10 | .47 | 60% | .2% |

plants. The stimulative effect of contact of one plant with another is shown in Fig. 2. The tomatoes in this case were grown in a well-lighted conservatory in soil similar in all respects and the water supplied was such that each plant obtained similar amounts. (Cf. Table 1.)

[1] 36 plants used.

## Response of Plants to Contact Stimulation with Wires and Twine

The investigations relating to the effects of contact with wires, etc., are given in Tables 2–9. All of these experiments were made in a well-lighted conservatory, the plants being grown in a good uniform grade of loam either in solid beds or in benches. In this series 1–6 plants were enclosed by wires, or dowels, and twine, and in some cases only fish netting was employed. The normal plants were in some instances grown free from contact with one another and in others not. In the case of only a single plant being surrounded by wire netting contact would occur only with the wire, whereas when two or more

Fig. 3. Showing growth of castor beans in contact and not in contact with wire netting. Plants removed with as little disturbance as possible from original position for photographic purpose.

plants were grown tolerably close together they would eventually be in contact with each other as well as with the wire netting, etc. Hence contact stimulation would result not only from the use of wires, etc., but from the contact of plants with one another, or in other words the so-called normal plants were not in all instances free from contact, inasmuch as when they were grown in groups they would eventually touch one another and growth would be influenced. We therefore have two series of experiments, namely: (*a*) those in which the

normal plants were perfectly free from contact with one another and (*b*) those in which the so-called normal plants were more or less in contact with one another. Both of these normal series were compared with those in direct contact with wires, etc. The plants in this series of experiments all show a gain in height by contact with different material. The effects of contact with wire netting (2-in. mesh) as compared with no contact whatsoever in the normal plants is given

FIG. 4. Showing growth of tomato plants in contact and not in contact with wire.

in Tables 2–4. In the former experiment (Table 2) 12 plants were utilized, all of which were grown separately, 6 being surrounded by cylinders of wire netting and 6 grown free from any contact whatsoever. The plants in contact with wire netting showed a gain in height of 31 percent compared with those of the normals and the same percentage gain is given in Table 3, in which case the contact plants

TABLE 2

*Showing Growth of Sunflowers (Helianthus annuus L.) in Contact with Wire Netting. Average of One Experiment with Twelve Plants*[2]

| | Average Height (Centimeters) | Percentage Gain in Height by Contact |
|---|---|---|
| Normal | 131.9 | |
| Contact wire | 173.0 | 31% |

TABLE 3

*Showing Growth of Sunflower (Helianthus annuus L.) in Rows between Wire Netting. Average of Two Experiments with 54 Plants*[3]

| | Average Dimension and Weight in Centimeters and Grams | | | |
|---|---|---|---|---|
| | Height | Internodes Length | Weight | Percentage Gain in Height by Contact |
| Normal | 114.1 | 6.9 | 307.9 | |
| Contact wire | 151.2 | 8.9 | 302.9 | 31% |

TABLE 4

*Showing Growth of Castor Bean (Ricinus communis L.) in Contact with Wire Netting*[4]

| | Average Dimension and Weight in Centimeters and Grams | | | | | |
|---|---|---|---|---|---|---|
| | Height | Diameter Stem | Internodes | | Weight | Percent Gain in Height by Contact |
| | | | Number | Length | | |
| Normal | 73 | 1.8 | 9.2 | 7.8 | 457 | |
| Contact wire | 99 | 1.5 | 8.1 | 12.3 | 284 | 35% |

were grown between parallel rows of wire netting, the netting being of sufficient distance apart to come in contact with the leaves of the plant. Neither the normal plants nor those in contact with the wire touched each other. The experiments with the castor beans shown in Table 4 were identical with those given in Table 2. This showed a gain of 35 percent in the contact plants over the normal. The remaining 5 tables (5–9) show the effects of surrounding plants with wire netting, dowels and twine, and fish netting. Since in this series, from 2–6 plants are grown close together, they also show to a certain extent the effects of contact with one another. Both the normal and contact plants were in pairs in Tables 5, 6 and 8a while 7 and 8b were arranged in threes and those in Table 9 contained 6 plants. In Table 7a, a wire netting was suspended overhead by twine and did not come in contact with the soil. From the data given in these tables it is hardly possible to draw exact deductions as to the relative

[2] Normal plants separated from one another.

[3] Normal plants separated from one another.

[4] 12 single plants used, 6 in contact and 6 not in contact.

value of the various methods employed in inducing responses to contact stimulation. Deductions, however, based upon a large series of experiments not included here justify us in stating that surrounding plants loosely and irregularly with twine does not produce the same degree of stimulation or response, as by the more thorough contact derived from the use of other material such as wire netting with a uniform mesh, or, in other words, plants react more pronouncedly to a larger contact surface than to a relatively smaller one, although there probably exists a definite size of mesh which would produce the best result, and this would undoubtedly vary with different species. There appears, however, to exist some difference in the degree of stimulation arising from the same size mesh, as shown by the behavior of some species when the contact is applied to the leaves. The leaves, for example, of the sunflower and corn do not respond so freely as those of tomatoes and the castor bean presumably because the leaf apices are the most sensitive as in the case of tendrils. The latter species, possessing different type leaves, would appear to act differently on this account.

TABLE 5

*Showing Growth of Castor Bean (Ricinus communis L.) in Contact with Wire Netting*[5]

| | Average Dimension and Weight in Centimeters and Grams | | | | | |
|---|---|---|---|---|---|---|
| | Height | Diameter Stem | Internodes | | Weight | Percentage Gain in Height by Contact |
| | | | Number | Length | | |
| Normal..... | 32.3 | 1.06 | 10.3 | 3.1 | 152 | |
| Contact wire... | 55.1 | 1.18 | 11.5 | 4.6 | 200 | 70% |

The data derived from these experiments are not sufficient to allow of deductions being drawn which would be of any value in determining the relative value of the various-sized meshes in stimulating growth. In some cases where galvanized iron netting with a one-inch mesh was employed, the stimulation appeared to be equally as great as with the two-inch mesh. Neither is it possible by these tests to determine accurately the difference in the degree of stimulation which resulted from the use of wires and that from the contact of the plants themselves. In all cases where single plants were employed they were removed far enough away from one another so as not to touch. The stimulated growth, therefore, was due entirely to the material which surrounded them. On the other hand when plants were grown in such a manner as to touch one another there existed two sources of contact. In the experiment shown in Table 9, six sunflower plants

[5] 12 plants used. Plants in pairs.

were grown close together (about 8 inches apart) and the two series of normal plants which consisted of twelve or six in each set were in contact with one another throughout their period of development. Hence, the percentage gain in growth in height is due to the additional contact of the plants to the various materials which surrounded them. The largest increase in growth is shown in Table 5 but this data was obtained only by the use of 12 plants and probably is exceptional. When closely grown plants are surrounded with wire netting, etc., and especially large-leafed plants such as the common sunflower the leaves do not have an opportunity to assume their normal shape and in this way there occurs a tendency to shade the stems. The displacement of the leaves by the wires thus shading the plants or the slight shadow cast by the wire enclosures apparently has little effect on the growth in length of the internodes, inasmuch as the same reactions can be obtained by growing the plants in darkness. The data concerning the results given in the tables (2–9) follow.

TABLE 6

*Showing Growth of Castor Bean (Ricinus communis* L.) *and Corn in Contact with Twine*[6]

| Experiments | Average Dimension, etc., in Centimeters | | | | |
|---|---|---|---|---|---|
| | No. of Plants Used | Height | Internodes | | Percentage Gain in Height by Contact |
| | | | Number | Length | |
| (*a*) Normal | 24 | 81.7 | 14.6 | 5.8 | |
| Contact twine | | 93.6 | 13.0 | 6.3 | 12% |
| Corn (*Zea Mays* L.) | | | | | |
| (*b*) Normal | 36 | 132.9 | 10.0 | 12.4 | |
| Contact twine | | 145.6 | 10.1 | 14.0 | 9% |

TABLE 7

*Showing Growth of Sunflower (Helianthus annuus L.). (a) Average of Twelve Plants in Contact with Wire Netting, (b) Average of Twelve Plants in Contact with Stakes (Dowels) and Twine*[7]

| Experiments | Average Height (Centimeters) | Percentage Gain in Height by Contact |
|---|---|---|
| (*a*) Normal | 137 | |
| Contact wire | 164 | 19% |
| (*b*) Normal | 132 | |
| Contact stakes and twine | 178 | 34% |

[6] Plants in pairs. 24 plants in (*a*), 36 in (*b*).

[7] Plants in triplets.

TABLE 8

*Showing Growth of Sunflower (Helianthus annuus L.) in Contact with Wire Netting*[8]

| Experiment | Average Dimensions and Weight in Centimeters and Grams | | | | | |
|---|---|---|---|---|---|---|
| | Height | Diameter Stems | Internodes | | Weight | Percent Gain in Height by Contact |
| | | | Number | Length | | |
| (*a*) Normal..... | 108.80 | 1.35 | 14.2 | 6.8 | 241.5 | |
| Contact wire.. | 138.91 | 1.33 | 14.8 | 10.4 | 267.9 | 27% |
| (*b*) Normal..... | 81.5 | 0.80 | 19.7 | 4.2 | 90.6 | |
| Contact wire.. | 109.2 | 0.84 | 24.5 | 4.5 | 92.6 | 33% |

TABLE 9

*Showing Growth of Sunflower (Helianthus annuus L.) Surrounded by Wire and Twine. 60 Plants Used in Each Test. Experiment Made in Greenhouse in Benches*[9]

| | Average Dimension and Weight in Centimeters and Grams | | | | | |
|---|---|---|---|---|---|---|
| | Height | Diameter | Internode Length | Weight | Moisture Percent | Percent Gain in Height by Contact |
| Normal..... | 132.5 | 1.59 | 8.03 | 213.3 | 87.6 | |
| Contact wire..... | 151.0 | 1.46 | 9.01 | 216.0 | 89.6 | 15% |
| Contact twine..... | 155.0 | 1.43 | 8.71 | 210.0 | 90.4 | 16% |
| Contact fish net... | 159.0 | 1.40 | 10.50 | 160.0 | 91.8 | 20% |

The average diameter of the stems of the normal was 1.2 cm. and for those in contact 1.24 cm. The average number of internodes for the normal was 13 and for the contact plants 13.6; while the average length of internodes for the normal was 6.8 cm. and that for the contact plants 8.9 cm. or a gain of 30 percent. The average weight for the normal plants was 243 grams and for the contact 216 grams. The diameter, number and length of internodes was slightly greater in the contact than in the normal. The average weight was 12 percent greater in the normal than in the contact plants. The moisture contents of the plants were greater in the contact plants than in the normal ones. The most important difference between the normal and contact plants is in the length of internodes.

## RESPONSE OF PLANTS TO CONTACT WITH EXCELSIOR

All of the experiments with excelsior were made with seedlings and were carried on in darkness. These were made in large flower pots containing either soil or sawdust. The excelsior was packed loosely over the soil or sawdust as the case might be at the time the seeds

[8] 12 plants used in each experiment. (*a*) Plants in pairs; (*b*) in triplets.

[9] Plants in sixes.

were planted, to a height of about 10 inches and often less, depending upon the nature of the plant in use. The excelsior was cut in lengths varying from 1 to 10 cm. or according to the nature of the plant employed. Since these experiments were all made in darkness and the plants were in all cases covered with receptacles, such factors as light and transpiration were controlled, and under these conditions the seedlings were dependent largely on the reserved material contained in the seeds. There was, however, no contact of the plants with each other. Moreover in this series, the same contact material was used throughout, namely excelsior, and any specific reaction which might arise from the use of different materials in contact with the

TABLE 10

*Showing Growth of Horse Beans (Vicia Faba L.) in Contact with Excelsior*[10]

| Experiments | Average Height and Weight in Centimeters and Grams | | | | |
|---|---|---|---|---|---|
| | No. of Plants Used | Height | Weight | Percentage Gain by Contact | |
| | | | | Height | Weight |
| (*a*) Normal | 149 | 14.03 | 0.96 | | |
| Contact excelsior | | 18.20 | 1.28 | 29% | 33% |
| (*b*) Normal | 374 | 15.10 | 0.74 | | |
| Contact excelsior | | 18.50 | 1.05 | 18% | 41% |
| (*c*) Normal | 122 | 17.32 | 1.37 | | |
| Contact excelsior | | 20.41 | 1.50 | 17% | 9% |
| Average normal | | 15.48 | 1.02 | | |
| Contact | | 19.03 | 1.61 | 23% | 58% |

TABLE 11

*Showing Growth of Hypocotyls of Lupines (Lupinus albus L.) in Contact with Excelsior. Average of Two Experiments with 128 Plants*[11]

| | Average Height of Hypocotyls (Centimeters) | |
|---|---|---|
| | Hypocotyls | Percentage Gain by Contact |
| Normal | 19.28 | |
| Contact excelsior | 21.65 | 12% |

plants would not be present in these. There would of course occur variations in the stimulus imparted to the different species owing to difference in the relative degree of contact of the plants with the excelsior—a feature which would be determined by the fineness, compactness and amount of the excelsior employed, as well as by the

[10] Experiments in which light was excluded.

[11] Experiments in which light was excluded.

surface area of the organs in touch with the same. Inasmuch as the plants used were seedlings and a larger number were employed than in the preceding series, the results are likely to be more uniform. On the other hand it should be noted that with the use of seedlings grown under good heat conditions (in which case they would develop rapidly) the duration of stimulus would be much less prolonged, and the ultimate effect of contact on the configuration of the plants would be less pronounced. The most marked stimulating effect of contact would occur in general in those experiments which were the most prolonged, namely with the larger seedlings. With the exception of corn all of the measurements given are either of the hypocotyls or stems. The results of these experiments are given in Tables 10–15, all of which show a stimulated growth due to contact with excelsior. The average weight in all instances where determined was greater in the contact than in the normal. In one water determination with lupine, there was 4 percent more moisture in the contact-stimulated plants than in the normal. In the experiments with corn (Table 14) measurements of leaves were taken as well as the cotyledons although it was our original intention to include in our measurements the cotyledons only, since when the leaves break through the cotyledons the growth of these organs is greatly retarded. The data giving the measurements of leaves in the corn, however, have a limited value as the growth of the leaves displayed more or less erratic behavior. In one experiment the leaves protruded above the excelsior and consequently they were not in contact. In another instance the leaves showed a very decidedly accelerated growth in the normal plants which was caused by a brief and accidental exposure to light. By taking proper precautions in further experiments this did not occur again. Some of the more sensitive cotyledons of the *Gramineae* are characterized by a marked growth correlation following mutilation or decapitation of the cotyledons in etiolated seedlings, and similar reactions occur to etiolated seedlings which are exposed to light. The function apparently of the cotyledons is to protect the true leaves in protruding upwards through the soil and as soon as they are exposed to light their growth ceases rather abruptly. Correlated with the retarded growth of the cotyledons is a greatly accelerated growth of the leaves which may amount to over 100 percent increase in two or three hours. The exposure of the cotyledons to light even for a brief period is sufficient to check their growth and greatly accelerate the development of the leaves and this is what happened on one occasion.

The normal plants would be the most affected by any such exposure as they were not covered with excelsior, while the contact plants

TABLE 12

*Showing Growth of Peas (Pisum sativum L.) in Contact with Excelsior. Average of Two Experiments with Eighty-two Plants*[12]

| | Average Height of Plants (Centimeters) | |
|---|---|---|
| | Stems | Percentage Gain by Contact |
| Normal | 13.07 | |
| Contact excelsior | 16.66 | 27% |

TABLE 13

*Showing Growth of Cucumbers (Hypocotyls) (Cucumis sativus L.) in Contact with Excelsior*[13]

| | Average Height of Hypocotyl (Centimeters) | |
|---|---|---|
| | Hypocotyls | Percentage Gain by Contact |
| Normal | 15.04 | |
| Contact excelsior | 16.30 | 8.3% |

were to a more or less extent protected from light by the excelsior. One of the experiments with lupines which was carried on at the same time behaved in a similar manner to that of corn. In one case 31 out of 36 of the normal plants developed leaves averaging 7 cm. in length while none developed in any of the excelsior contact plants—a feature due to the same cause, namely, to a brief and accidental exposure of the plants to light.

TABLE 14

*Showing Growth of Cotyledons and Leaves of Corn (Zea Mays L.) in Contact with Excelsior. Average of Two Experiments with 72 Plants*[14]

| | Average Length of Cotyledons and Leaves (Centimeters) | | | |
|---|---|---|---|---|
| | | | Percentage of Gain by Contact | |
| | Cotyledons | Leaves | Cotyledons | Leaves |
| Normal | 8.41 | 17.75 | | |
| Contact excelsior | 10.07 | 18.44 | 19% | 4% |

TABLE 15

*Showing Growth of Turnip (Hypocotyls) (Brassica Rapa L.) in Contact with Excelsior. Average of Two Experiments with 194 Plants*[15]

| | Average Height of Hypocotyls (Centimeters) | |
|---|---|---|
| | Hypocotyls | Percentage Gain by Contact |
| Normal | 8.57 | |
| Contact excelsior | 9.66 | 11% |

[12] Experiments in which light was excluded.
[13] Experiments in which light was excluded. No. of plants used 26.
[14] Experiments in which light was excluded.
[15] Experiments in which light was excluded.

## Response of Roots to Contact Stimulation

### *Excelsior*

In the experiments so far enumerated no account has been taken as to the effects which various substances coming in contact with stems may have upon the growth of roots and other organs. It is quite natural to expect that if one organ is affected by a stimulus other organs will be, inasmuch as the organism as a whole responds to stimuli of quite insignificant character. Incidentally, we observed in our early experiments with seedlings grown in sawdust that the roots in some cases respond when the serial portions of the plant were in contact with excelsior. In 1912 experiments were carried on for the purpose of comparing the growth of roots in soil under different conditions. These experiments consisted in the growing of roots in boxes with glass sides. In one series the roots were grown in holes or channels along the edge of the glass, and in the other series no holes were provided. In both series there would be contact, but where the roots followed the channels, there was less contact of the roots with the soil particles than where they had to force themselves through the soil. These experiments being limited, however, did not furnish data of any particular value, although from the more or less meager data obtained, they seemed to indicate that the presence of grooves or channels in the soil produces less stimulating effect on the growth of roots than when more thorough contact exists. Most of our investigations relating to the effects of contact on roots were made with excelsior, and in some cases sphagnum moss and cocoa fibers were used. In many experiments we have also utilized various-sized particles of gravel, sand, and silt suspended in water. The excelsior which we employed did not produce any bad effect on the growth of roots when submerged in water. On the other hand it appeared to clear up the water in some instances, inasmuch as it was apparent that it absorbed certain accumulated products which sometimes occurred, and which were more or less detrimental to the growth of the roots. The water containing the excelsior cultures was clearer and possessed a more agreeable odor than those cultures where it was not used. As the seeds were suspended over water on a fine-mesh cotton cloth netting, these would occasionally become too moist and in this way the water became more or less turbid, owing to the presence of various extract substances derived from the same. The presence of excelsior in the water had a tendency to prevent any abnormality in the growth of the roots which might follow from the presence of foreign substances, and in this respect it acted like sand and charcoal in removing certain impurities such as copper sulphate.

TABLE 16

*Showing Growth of Roots of Lupines (Lupinus luteus L.) in Water Containing Excelsior and Sphagnum Moss*[16]

| Treatment | Average Length of Primary Roots (Centimeters) Roots |
|---|---|
| Normal | 7.3 |
| Sphagnum moss | 8.8 |
| Excelsior coarse | 10.4 |

For the purpose of obtaining more uniform conditions for root growth, we subsequently adopted larger containers provided with loose partitions, in which case all the plants were subject to like conditions. The excelsior experiments were made in either glass or earthen jars with tap water which had been previously boiled to exclude the air. The excelsior, which was of the ordinary commercial form, was in long strands of more or less irregular shape and in cross section was about 1 mm. in diameter. We employed three different grades, namely, the coarse, loose, curly form as it is obtained commercially, and the same cut from 1 cm. to 4 cm. long. The uncut grades were packed loosely in the jars containing the water, while the finer grades were much more compact and greatly increased the contact surface to which the roots were subjected. In all cases the excelsior was boiled before using it to exclude air, inasmuch as the presence of air would be capable of modifying growth. The seeds employed were of a good quality and were separated by sieves and carefully selected before planting, which insured a uniform size and

TABLE 17

*Showing Growth of Stems and Roots of Peas (Pisum sativum L.) in Water Containing Excelsior. Average of Four Experiments*[17]

| Treatment | Average Length of Stems and Primary Roots (Centimeters) Stems | Roots |
|---|---|---|
| Normal | 11.2 | 4.5 |
| Excelsior coarse | 10.3 | 7.0 |
| Excelsior fine | 11.1 | 8.8 |

Secondary roots predominated in the fine excelsior, many in the coarse excelsior, practically absent in the normal.

corresponding germinating capacity. The experiments were conducted in a dark place, although in this series not in absolute darkness. The amount of light, however, which prevailed was insufficient for photosynthesis or for phototropic curvatures. Neither the stems nor roots were in contact with one another, hence, any stimulating growth

[16] 5 plants used in each test.

[17] One hundred and sixty plants used.

which followed was due to the excelsior alone. All of the plants were in the seedling stage and the duration of the experiments in no case exceeded fifteen days. The investigations relating to contact stimulation of roots were limited to the use of a few species which show different types of reaction. The results of these experiments are shown in Tables 16–18, although several other species were employed which are not included here. In all cases, the "excelsior coarse" implied the loose commercial form which came in contact with roots occasionally, while "excelsior fine" was in these particular experiments, cut up into lengths 4 cm. long and furnished considerable contact. When such plants as lupines and peas which possess strong and fairly good-sized primary roots were in contact with excelsior the reaction was characterized mainly by an accelerated growth of the primary root system, together with considerable secondary root development whereas in the case of delicate roots, such as mustard (Table 18 ), the growth of the primary roots is less and the secondary root development is greatly accelerated. Practically little or no difference existed in the growth of hypocotyls and stems in any case, although this feature is not always constant. In both the lupines and peas (Tables 16 and 17) there occurred a considerable accelerated growth of the primary roots. In the latter case (Table 17), which represents an average of four experiments, there was a decided increase in the number and length of secondary roots from the normal to the fine excelsior. In one experiment where the secondary roots were counted, their average number was as follows:

| | |
|---|---|
| Normal | 17 |
| Coarse excelsior | 32 |
| Fine excelsior | 40 |

This feature was more pronounced in the mustard, however, where the primary roots in contact with the excelsior were much less de-

TABLE 18

*Showing Growth of Hypocotyls and Roots of Mustard (Brassica alba Boiss.) in Water Containing Excelsior*[18]

| | Average Length of Hypocotyls and Primary Roots (Centimeters) | |
|---|---|---|
| Treatment | Hypocotyls | Roots |
| Normal | 12.1 | 11.1 |
| Excelsior coarse | 13.3 | 6.8 |
| Excelsior fine | 11.9 | 8.9 |

veloped (Table 18). In this case there were no secondary roots on the normal plants; many in the coarse excelsior and very numerous

[18] 20 plants used in each test.

and well developed on those in contact with fine excelsior. The number of secondary roots or those in contact with the fine excelsior averaged 18 to a plant and the ratio of the total length of the entire root system of the normal and fine excelsior was 1 to 6 in favor of the latter. Measurements made of the total surface area of a single typical root from one of the normals and one of the fine excelsior showed that the total surface area of the latter was over three times that of the normals. These experiments show, at least in young seedlings, that roots respond to contact and that the response is confined very largely to these organs, although more than one type of growth correlation may occur. They indicate also that different species will respond to contact in a different manner. In other words, secondary root development is stimulated more in some species than in others by contact, and this excessive development of the secondary root system is correlated with a lesser development of the primary root system.

*Soil Particles*

Since roots are sensitive to contact to various materials it would naturally be supposed that the nature of the soil constituents or particles would exert an influence upon growth and configuration of plants, and particularly upon the root itself. As contact is effected by the surface area involved, variation in the size and shape of the soil particles would be expected to produce different results. Consequently, a series of experiments were carried on, but not completed, with the idea of determining what effect, if any, soil particles have on the growth of roots, and how the various-sized particles effect development. For this purpose we had at our disposal several carefully prepared grades of gravel, sand, silt and clay which had been sifted through sieves and bolting cloth. The size of the particles ranged from 16 mm. to 0.1 mm. and in some cases to .05 mm. The experiments were conducted in glass jars filled with water previously boiled to exclude air. Each jar was completely filled with some particular grade of material which had previously been thoroughly washed with water and sterilized. We thus had a medium in which the particles of gravel, sand, etc., were surrounded by water, and as far as possible free from air. A fine-mesh cotton netting was placed over the jars on which rested the seeds, and as germination took place the radicles penetrated downward between the submerged soil particles. All experiments made with soil particles in water were carried on in darkness in a moist chamber where transpiration was limited and the temperature condition alike. The plants were in fact under identical conditions throughout, except as regards the substratum.

The normal or check series were run in water alone. The results given by these experiments, which were limited in numbers, are similar to those obtained by the use of excelsior in contact with roots in water, namely, the various grades of gravel, sand, and silt gave rise to different reactions on the part of the organism which resulted in a stimulated growth correlation, as exemplified in the development of the primary organs and secondary root system. The results obtained by the use of mustard, peas and soy beans, etc., in the experiments so far carried on, indicate generally that there exists little difference in the height of the hypocotyls or stems of the normals, and those in contact with the different-sized particles of soil constituents. The growth in length of the primary root is lessened and the secondary root system is greatly increased as we approach the finer grades of contact material. In some species with relatively large roots the coarser particles, namely 16–8 mm., appear occasionally to stimulate primary organs, but this reaction is variable, and associated with growth correlations as manifested in the more or less increased development of the secondary root system. The reaction of roots to different-sized particles will undoubtedly be found quite variable. Species with relatively large and strong primary roots such as the horse bean, peas, etc., react differently from seedlings with a delicate root system, such as the mustard and turnip. The roots of the latter species, even when grown in contact with excelsior or soil particles, produce a marked secondary root system characterized by little or

TABLE 19

*Showing Growth of Hypocotyls and Roots of Mustard (Brassica alba Boiss.) in Contact with Different-sized Particles of Sand and Gravel in Water*[19]

| Size of Particles (Millimeters) | Average Length of Hypocotyls and Primary Roots (Centimeters) | |
|---|---|---|
| | Hypocotyls | Roots |
| Normal | 8.7 | 12.7 |
| 16–8 | 8.2 | 12.6 |
| 8–4 | 11.7 | 8.7 |
| 4–2 | 11.5 | 7.6 |
| 2–1 | 11.9 | 4.4 |
| 1–0.5 | 11.6 | 4.3 |
| 0.5–0.25 | 11.2 | 4.2 |
| 0.25–0.1 | 13.7 | 3.4 |

no primary root development. The same tendency exists in species characterized by larger roots to increase their secondary root system. On the other hand, the primary root system is greatly accelerated by contact with excelsior in species with large roots. (Cf. Tables 16–17 and 18.) The experiments with mustard given in Table 19 show

[19] 15 plants used in each test.

much difference in the growth of hypocotyls and roots in the different grades. This feature is associated with the greatly accelerated development of the secondary root system, and extending from the coarser grades to the finer ones. Other than the production of secondary roots in the plants in the 16–8 mm. grades there was little difference between the growth of the latter and those of the normal.

There were no secondary roots in the normal grades or water culture plants in this case, although they were fairly well established in the 16–8 mm. grade, from which grade the increase in numbers and total length of the secondary roots were quite noticeable. The average development of the primary and secondary organs as well as the surface area of the same was greater in the contact plants than in the normals. Soil particles and excelsior submerged in water have a similar stimulating effect on mustard as will be seen by comparing Tables 18 and 19.

## Theoretical Considerations

While the general tendency of plants and plant organs is to avoid contact with one another, the histological units or cells which composed the individual are in contact with one another, and the same holds true to a certain extent with different organs when in the embryonic or bud stage. It is the exception rather than the rule to find the various members or organs of different plants, or even those of the same plant such as roots, branches, leaves, etc., in contact with one another, or in other words it appears to be a universal law in nature that the various organs of plants occupy space by themselves. Uniformity and regularity in the arrangement of cells and organs is more common to the lower than to higher organisms, since in the higher organisms this feature is sacrificed to some extent by biological necessity and adaptation. Primarily the arrangements of organs in plants or angles of divergence are determined by laws which are common to gravitational and electro-magnetic phenomena, and the arrangement of the various organs of plants appears to be determined by the action of these forces upon their ultimate structural units, molecules, micellae, atoms, electrons, or whatever they may be. The angles which various organs assume in plants closely resemble those which are illustrated in the formation of certain types of crystals, and the behavior of iron filings under the influence of a magnet. Plants are susceptible to all of the common environmental influences which surround them, but the *modus operandi* of these various external agencies on protoplasm is little known and especially concerning the mechanism and nature of conductivity of impulses. The reaction to contact results from a mechanical impulse, inasmuch as when the

external cells of the organism come in contact with solid particles a reaction follows. To affirm, however, that the stimulus is mechanical in nature does not explain anything, because we know nothing of the nature of the so-called mechanical impulse. The bombardment of organisms with electric waves (negative electrotropic response) may be of the nature of a mechanical impulse and such may hold true for other forms of radiant energy. Phototropic, thermotropic, electrotropic and contact stimuli may not materially differ from one another in the nature of their action on organisms, that is, in the sense of acting in a mechanical manner on plants. The stimulation resulting from such contact is apparently transmitted to the living zones which induce definite adjustments or coordinations of the vital processes, the nature of the response being determined by the nature of the stimulus involved and the organs stimulated. The external cells of a leaf, for example, coming in contact with an object would probably react to the stimulus through the cuticle and exterior cell walls. The reaction of plants to contact is probably one of the most primitive forms of responses and quite universal in the vegetable kingdom.[20] The nature of the response to contact resembles mostly that of touch or at least a primitive and rudimentary form of this sense.

There are several types of contact stimulation that have long been recognized such as occur in the response of tendrils, tentacles, stamens, etc., when brought in contact with different substances. These reactions are associated with different types of irritability. Most of the known reactions to contact such as are illustrated by tendrils, etc., are closely associated with biological adaptations, and as such they have been subject to considerable modification. It is not at all improbable, however, that these various types of reactions are modifications and differentiations of a more simple and universal form of contact response. The various forms of response movements which are associated with irritability have been classified under the so-called tropistic, nastic, and taxic reactions. The first type of response is characterized by the movement of organs toward a definite position in response to a stimulus, while nastic reactions are those which are independent of the direction of the stimulus. Taxic reactions are those shown by motile organisms. There are several different types or manifestations of irritable phenomenona such as photo-

[20] Some experiments made with mucor in Petri dishes containing beef extract and fine particles of quartz sand showed contact responses. Both series of Petri dishes contained the same amount of beef extract, but in one the fine sand was added for the purpose of obtaining contact with the mycelium. The sporangia were black and mature in the Petri dishes without sand, while in the dishes containing the fine sand, the aerial hyphae were much more elongated and the sporangia light in color and less mature.

tropism, geotropism, etc., which are characterized by both positive and negative reactions, but for our purpose it is necessary to consider only a few which are somewhat similar in character, and which have not unlikely originated from a simple fundamental type.

### (*a*) *Contact Stimulation*

Probably a universal type and one of the most fundamental forms of response in plants, which is characterized by a stimulated growth of various organs due to contact of one organ with another, or with various substances. The extent of the reaction is determined by the degree of contact, and probably influenced by the nature of the contact substance.

### (*b*) *Haptotropism*

Illustrated by various tendrils reactions; tentacles of *Drosera*.

### (*c*) *Haptonastie*

Illustrated by certain types of contact of some tendrils and tentacles of *Drosera*.[21]

### (*d*) *Seismonastie*

Illustrated by movement of stamens of *Centaurea*, *Berberis*, and *Mimosa* leaves.

### (*e*) *Thigmotaxis*

Reaction of motile organisms (*Chlamydomonas*) resulting from contact of cilia with different substances.

### (*f*) *Wound Stimuli and Reactions*

Wound stimuli in general caused by mutilation, presence of organisms, and direct contact of plant members with one another induce various reactions, the nature of which depends upon the host plant, and nature of the cause responsible for the same. The general response to wound stimulation is manifested by the production of abnormal growth due to active cell division, and in some cases enlargement of the cells. These reactions are characterized by local effects and the reactions are often disproportionate to the stimulus.

In some types of reactions there would seem to be involved more than one class of phenomena. For example, the haptotropistic reactions of tendrils, or at least the subsequent effects involved in the formation of the spiral, etc., by the stimulus, and which is manifested

[21] Stark (3) has observed that many plants and some roots react to contact stimulation similar to tendrils when rubbed with a stick or cork.

by the production of mechanical tissue would seem to be similar to that induced by other irritable phenomenona. In the formation of the spirals in tendrils there is considerable stress to be overcome and the constantly increasing weight of the various members of the plant, such as is associated with the development of foliage, fruit, etc., together with the effects of rain, swaying movements due to wind, is most admirably met by the production of mechanical tissues. These additional strains are taken care of by the same type of response as that induced by the stretching of plants with weights. Since the leaves of plants appear to be quite sensitive to contact it is readily conceivable how the more specialized haptotropistic responses to contact exemplified by tendrils could readily be evolved from simple contact irritability. There are, however, a large class including various types of reaction phenomena which do not fall under tropistic, nastic and taxic responses. These are the so-called wound reactions—traumatotaxis (reaction of cell nucleus). Traumatotropisms, illustrated by decapitated root, and positive galvanic currents on roots, are apparently direct responses to wound stimuli, as probably are the reactions first observed by Darwin resulting from the attachment of different substances to the root tip. In wound reactions, however, contact is involved to a greater or less extent, and more or less injury and abnormal conditions are associated with this class of phenomena. Most of the responses following wounds are local in their effect, although the organism as a whole may be affected even from relative insignificant mechanical injuries, as shown by the modification in the developments and functions of the several organs in mutilated plants.

Representative types of this class are seen in the various accelerated growths produced by insects, fungi, bacteria, mechanical injuries, etc., and generally the reaction continues long after the primary or excitory cause has disappeared. Local accelerated growths, however, do not always follow as a result of the intrusion of pathogenic organism inasmuch as the nature of the response is determined to a large extent by the character of the tissue affected. For example, eel-worm infestation of roots may give rise to galls, whereas on stems such a response may not necessarily follow and even on roots these reactions differ. In many so-called wound reactions the degree of response is disproportionate to the stimulus responsible for the same. This is illustrated by feeble lightning discharges on trees, in which case the stimulus (lightning causing burning) lasts but a few thousandths of a second. The reaction, however, to such insignificant injury—often hardly perceptible and characterized by the destruction of a few cambium cells, may manifest itself for years in an accelerated growth of the annular rings adjacent to the injury. The flow of tissue in

sucker growth around stumps, the enclosure of twigs, grass, etc., by mushrooms, and the imbedding of tree guards illustrate stimulated growth responses not generally associated with wounding. When more or less long stubs remain following the destruction of limbs on trees, they act as a stimulus, and large masses of tissue ultimately accumulate around the base of the same. If, however, the stub is removed close to the tree, healing follows, and when the callus unites growth becomes normal. Again the feathery growths, consisting of small twigs which are common on the trunks of elm trees, give rise to the same type of reactions, namely, the formation of excrescence or tuberous growths at their point of junction to the tree. The presence of blocks of wood on trees to prevent the contact of guy wires with the bark often stimulates the flow of tissue, and while there is apparently no injury associated with this connection there exists a more or less severe tension or pressure on the bark. The tendency of tissue to grow over even loosely attached tree guards and wire attachments, even when it would require but little force to dislocate them, is universal. Signboards placed on trees, although often insecurely attached, are sometimes entirely obliterated by a greatly stimulated callous growth, and tree guards loosely attached to trees often become imbedded in the tissues, when it would require but little exertion on the part of the underlying tissue to dispose of the same. It may be assumed, however, that the presence of nails driven into the wood for the purpose of holding the sign in place would act as a stimulus, but the same reaction follows if the nails are not present and the sign merely held securely by means of wires. Moreover, the growth response here conforms to the sign as a whole rather than to any particular point of attachment by the use of nails, etc. Similar response occurs in the growing of roots around large masses of gravel in the soil or when limbs or roots come in contact with one another, in which case natural grafts may occur. The tissue, however, exterior to that which is in contact is often destroyed in natural grafts, etc., which would have the same effect as wounds; although even here the growth stimulation is much greater than that resulting from mere wounding. In this type of response there are two factors involved, namely contact and growth acceleration. The reaction, however, is local and does not differ materially whether injuries occur or not, as is shown by growth stimulations arising from other causes, such as frost cracks, etc. There are other similar types of reactions apparently differing somewhat in the nature of the response to contact from those enumerated, namely, those arising from restricted growth. Contact in such cases occurs, but injury may be absent, although abnormal growth may result. This type seems to be characterized in their manner of responding by a greatly increased osmotic tension of the cells.

When roots are growing between large boulders and are restricted in their development, the flow of tissue is such that the root may become enormously flattened. The reaction in such cases is similar to that produced by a wound, although evidence of wounding may be entirely absent. Such roots, however, often lift enormous weights which would indicate that considerable osmotic tension exists in the cells. When rapidly developing organs, such as a squash, for example, is placed in a harness and subject to weight, it will assume a much distorted shape which illustrates stimulated growth phenomena. Again, when ferns and even delicate mushrooms push through concrete they show little or no evidence of wounding, although the reactions in such cases are characterized by a large increase in the osmotic tension of the cell, sometimes equaling 50 atmospheres (4). The experiments of Pfeffer (5), in enclosing roots in plaster casts, thus restricting growth and greatly increasing the osmotic tension of the cells, are typical of this class of responses. To what extent, if any, cell fusion of sexual elements, development of attachment organs in fungi and algae, and outgrowths in spirogyra filaments when in contact with certain crystals, are related to contact, is problematical since in some instances chemotropic phenomena would have to be carefully differentiated from any other which might prevail in interpreting such phenomena. Also to what extent contact stimulation may influence cell enlargement and cell division resulting from the intrusion of foreign elements would be merely a matter of speculation at the present time. There are, however, numerous instances of cell enlargement associated with crystals (raphides), pathogenic and non-pathogenic organisms, which resemble contact stimulation, although the recent important contributions on this subject by Dr. E. F. Smith (6) would indicate, in some cases at least, that cell responses to pathogenic organisms are associated with chemical or physical phenomena. Some of the responses of plants associated with pathological phenomena are not characterized by cell stimulation, but with color reactions due apparently to excretions from organisms. Intense color reactions are also associated with marked cell proliferation caused by chemical substances absorbed by plants from the soil, as shown by the reactions of *Platanus Orientalis* to the toxic properties contained in illuminating gas. These reactions, however, as are similar ones in poplars and willows, which develop large masses of parenchyma under the bark and cause rupture of the same, are associated with two factors, namely, the direct effect of the toxic substances on the cambium inducing rapid cell division, and decrease in the tissue tensions of the cortex following the collapse of the same by poisons. Various chemical substances (banding substances) applied to trees produce local growth

acceleration, but these apparently affect the outer tissues, and to a certain extent the underlying vital layer. Dr. H. von Schrenk (7) and Dr. E. F. Smith (6) have shown that ammonia compounds cause intumescences in cauliflower. The absorption of the chemical substances by the roots in some cases produces a rupturing of the epidermal tissue which is followed by cork formation, and in cases of malnutrition excrescences are often formed on the fruit. Finally, contact stimulation has an important bearing on experimental work, especially with that done with plant food, fertilizers or soils, inasmuch as stakes and wires are often employed as support. Any differences existing in the contact of the plants, either by the use of supports or that occasioned by the proximity of plants to one another, thus causing contact, would be effective in modifying the results. The relative height and development of two plants which would affect the contact surface would also be important factors in experiments of this nature. Indeed in this respect we have noticed on more than one occasion experiments where differences existing in the degree of contact would account for all the variations in the growth of the plants that were supposed to be due to other causes rather than to the particular treatment which they received.

## LITERATURE CITED

1. **Hall, A. D., Brenchley, W. E., and Underwood, S. M.** The Soil Solution and the Mineral Constitutions of the Soil. The Jour. of Agr. Sci. 6: 278–301. Sept. 1914.
2. **True, R. H., and Oglevee, C. S.** The Effects of the Presence of Insoluble Substances on the Toxic Action of Poisons. Bot. Gaz. 39: 1–21. 1905.
3. **Stark, Peter.** Ber. d. d. Bot. Ges. $33^8$: 389.
4. **Stone, George E.** The Power of Growth Exhibited by Ferns. Bull. Torrey Bot. Club 36: 221–225. May 1909.
5. **Pfeffer, W.** Druck und Arbeitsleistung durch Wachsendepflanzen, p. 93.
6. **Smith, E. F.** Mechanism of Tumor Growth in Crowngall. Jour. of Agr. Res. 8: Jan. 1917.
7. **Schrenk, H. von.** Intumescences Found as a Result of Chemical Stimulation. Ann. Rept. Mo. Bot. Gard. 16: 125–148. 1905.

# DUPLICATION AND COHESION IN THE MAIN AXIS IN CICHORIUM INTYBUS

A. B. STOUT

*New York Botanical Garden*

The terms duplication and cohesion may be used to designate a very special type of fasciation which the writer has observed in the variety of chicory cultivated under the name "red-leaved Treviso." The most distinctive characteristic of this type of fasciation is the duplex nature of the main axis. From a single root a double stem arises with the two parts, as a rule, strongly united. The duplex nature is indicated by a pair of grooves which extend in the direction of the long axis and round out the two stem-elements. This is quite well shown in number 5 of the accompanying plate XII.

This type of fasciation differs from the banded and cone types most usually seen in that here two stem-elements of equal size and rank are clearly in evidence throughout a segment of unequal diameters, giving a symmetry that is bilateral. Also the fasciation is confined to the middle and lower portions of the stem and decreases upwards, the main axis often becoming at its apex quite symmetrically simplex.

I have been unable to find in the literature any reference definitely mentioning fasciation of this particular type. It appears not to have been noted and described even in this rather well-known variety of chicory.

In the degree and the extent of the duplication there is much variation. The most extreme condition of duplication is seen in the complete separation of the two stem-elements with each perfectly formed and without lesions, as is shown in no. 7 of Plate XII. In many cases the two elements are indicated only by grooves which extend from close to the base of the plant to a height of about three feet. The length of the grooves and the corresponding segment of evident duplication may, however, be reduced to mere traces, as is shown in no. 3 at *a* or in no. 4 from *a* to *b*, as indicated. In a few plants of this strain there is no evidence of duplication and the phyllotaxy is of a single and regular spiral only.

Each stem-element has its own phyllotaxy in so far as this can be expressed. In the most pronounced duplex condition there are clearly two separate spirals in evidence. The phyllotaxy of one is not a

continuation of the other and more branches and leaves are produced upon the two than upon a single stem. Branches and leaves occasionally develop, however, from the very center of the grooves and the bases of leaves thus placed often extend across a side of both stem-elements. Such leaves and branches are always simple as far as I have observed. In the uppermost portions of the stem the phyllotaxy is often completely regular, but immediately above the segment of noticeable duplication the phyllotaxy is irregular and this irregularity may extend to the apex or terminate in the banded type of fasciation.

Torsion is frequently seen. The two elements may twist about one another in spirals with the two parts equal in development and the spirals in the same direction. In other cases the two stem-elements exhibit incompatible growth either as to direction of torsion or rate of growth, or both, and mechanical lesions result. These tear apart the two elements or often cause one to break, thus producing much irregular and twisted development of the main axis. Various conditions which thus arise are shown in Plate XII. Usually the lateral branches above such lesions are poorly developed (no. 9), the more vigorous growth being seen in the lower laterals.

In this strain of red-leaved Treviso, irregularities of development are seen in the growth of the cotyledons. For most seedlings two quite normal and separate cotyledons are produced as shown in nos. 1, 2, and 4 of Text Fig. 1. In numerous cases even of sister plants the two cotyledons are fused; only the basal portions of the stems may be fused as in nos. 5, 6 and 15, or the fusion may extend upward toward the apex as shown in nos. 7, 8 and 9. In some cases what appears to be only one cotyledon is in evidence, as shown in nos. 10, 11, 12 and 16; either the two have become completely fused or the growing point of one failed to develop. The very complete series of stages of fusion leading to a single cotyledon suggests that the initial growing points of the two cotyledons may completely fuse or perhaps are never differentiated. There are also numerous cases of crumpled and irregularly developed cotyledons either in one or both of a pair or in a single one, as may be seen in nos. 3, 13, 14, 15 and 17.

In only two cases have I observed any tendency to an increase of cotyledons; in each of these seedlings one of the cotyledons was somewhat bisected, as shown in nos. 19 and 20. The duplication seen in the main axis is not accompanied by duplication or increase in the normal number of cotyledons.

In a very few instances there is no development of the plumule. This may occur in seedlings having two normal unfused cotyledons as

shown in no. 4, as well as in seedlings having only one cotyledon, as shown in nos. 16 and 17. Such plants usually die soon. In some cases, however, adventitious buds arise, but as far as observed these make only a feeble growth. The drawings 16*b* and 17*b* show such feeble adventitious growth of seedlings nearly three months old, at which time many sister plants had rosettes measuring ten inches in diameter.

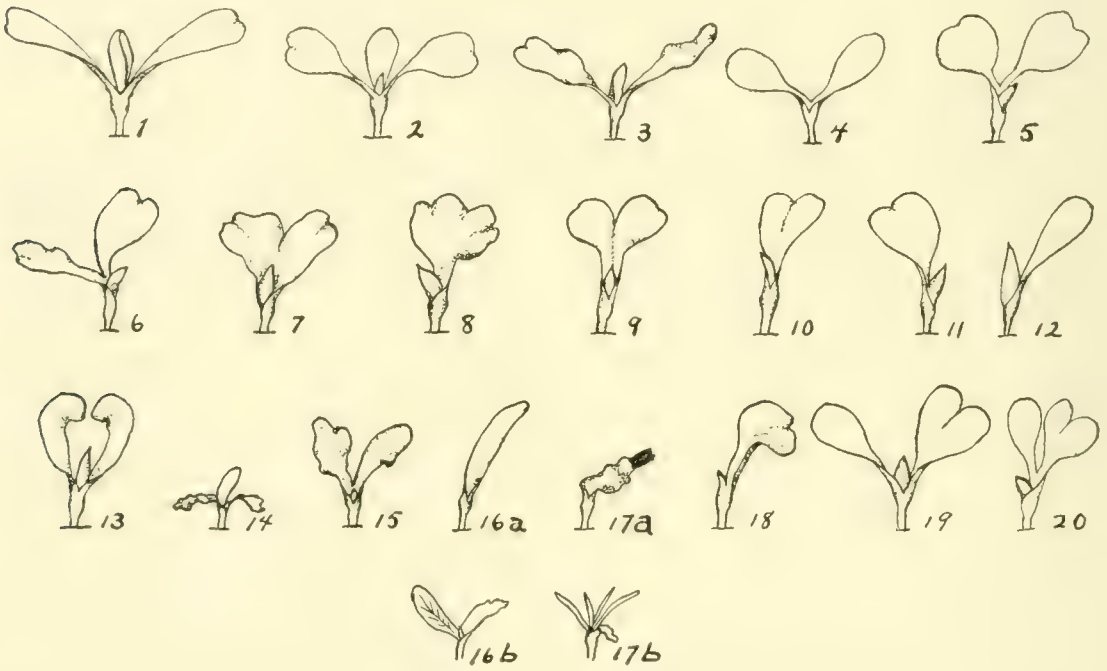



FIG. 1. Young seedlings of the variety red-leaved Treviso. Scale about one-half natural size.

1 and 2. Two normal separated cotyledons with plumule.

3. Two cotyledons, both somewhat crumpled.

4. Two cotyledons; no plumule.

5. Cohesion at base of cotyledons only.

6. Cohesion at base of cotyledons; one crumpled.

7, 8, 9. Decided cohesion.

10, 11, 12. Only one cotyledon present.

13. Two cotyledons; separation involved some lesion.

14. Much crumpled and poorly developed cotyledons.

15. Some cohesion at base.

16*a*. Single cotyledon; no plumule. *b*. Same seedling two months later with adventitious bud.

17*a*. Single much crumpled cotyledon with seed coat attached at apex; no plumule. *b*. Same seedling two months later.

18. Much fusion of cotyledons.

19, 20. Decided lobing of one cotyledon.

The growth interrelations of reduction or fusion of cotyledons with duplication in the main axis are not clear. In the former there is a fusion or reduction in the number of organs normally formed; in the latter there is a tendency to the production of two main stems

instead of one, accompanied by their cohesion or incomplete separation. In both the factor of cohesion is present, but in the cotyledons it leads to reduction in the number normal to the species, while in the stem it tends to reduce the duplication to the single stem-element that is normal to the species.

The occurrence of the sort of duplication described above has now been observed in four generations. Thirty-five plants of the 1913 crop of the variety red-leaved Treviso were grown from commercial seed. In 14 plants the main axes were decidedly duplex, the length of the segments showing duplication ranging from a few inches to about three feet. The stems of the other 21 plants showed no sign of duplication. All plants of this generation which were tested were found self-sterile from physiological incompatibility, so it was not possible to obtain self-fertilized seed. Numerous crosses were attempted between plants, but only one cross attempted was compatible.

In 1914, 12 plants were grown as progeny of the cross between two plants which were quite alike in exhibiting duplication of rather intermediate development. In all 12, duplication developed. The variability in degree of duplication was marked and ranged from very slight indications to very decided cases of torsion and lesion. One plant developed too late in the season to be tested for self-fertility, but the other 11 were all self-sterile. However, some compatible crosses were made from which 43 plants were grown in 1915.

Of the 1915 crop, 39 of the 43 plants exhibited duplication to some degree. In one plant the two elements were completely separate from the very base upward (no. 7). In several plants torsions and lesions were strongly developed. Four plants were apparently not in the least fasciated and in each of these the phyllotaxy was regular and single.

In the 1916 crop, 150 plants were grown. Two of these were from a self-fertile plant (the only one of the 1915 crop that was found to be self-compatible in any degree). The 148 other plants of this generation were from six different crosses involving eight different parent plants, all of which, however, exhibited duplication in some degree. This generation was descended from three generations of parentage that exhibited duplication. There was duplication to some extent at least in 144 of these plants. Six appeared to have a single stem-element with regular phyllotaxy; these six plants were distributed among the offspring of three different crosses.

One plant of the 1916 crop exhibited a noticeable fasciation of the ribbon type in the upper branches in addition to duplication and cohesion in the main axis. The tips of the main branch and of various laterals were broadly flattened and the branching was reduced so that

flowers and short spur branches were clustered at the extreme ends, giving a peculiar rosette-like appearance. The two types of fasciation were quite distinct on the plant, both as to general appearance and location.

From the performance of these pedigreed cultures, it seems clear that the character of duplication and cohesion persists in successive generations of this variety of chicory to such an extent as to appear strongly heritable. It is not completely so, for a few normal single-stemmed plants do occur quite irregularly in various generations and lines of descent.

The heredity of the character of duplication has also been tested by crossing plants of the 1915 crop showing typical fasciation with a plant of wild stock (plant *A*) which had a short, slender, main stem. No tendency to duplication has been seen in plants of wild stock which have been grown or in plants of various generations derived by crossing the wild plant *A* with plants of the cultivated variety known as Barbe de Capucin. This cross here in question involved, therefore, on one side parents with duplication, and on the other a plant of a stock free from duplication.

Thus far 81 plants of an $F_1$ generation have been grown; nineteen of these had the wild plant *A* as a seed parent. Of these 81 plants only three possessed the grooves which are seen in most typical cases of duplication of the main axis. In only one of these were the grooves pronounced (see no. 10); in the other two there were only slight indications of grooves (see no. 11). In 78 plants there was not the slightest indication by grooves of any duplication. However, in tracing the phyllotaxy from base upward, irregularities were seen in 48 plants. Two leaves or branches were often opposite or the direction of the spiral would appear to shift from left to right or vice versa. In 30 plants the spiral of the phyllotaxy proceeded very regularly from base to tip in a way that indicated a normal single stem-element (see no. 12). Of the 19 plants having the wild plant for a seed parent, 7 were quite normal and in 12 there was a mixed or irregular phyllotaxy.

Judged by performance in the $F_1$ generation, the character of duplication is only incompletely and partially dominant. An intermediate type is frequent in which the only suggestion of a duplex condition of the main axis is seen in an irregular phyllotaxy.

I cannot at the present time contribute any information regarding the sources, causes, or nature of the stimulus operating in duplication nor any definite facts regarding the attending anatomical development. When this paper was presented it was suggested by Dr. Erwin F. Smith that possibly infection by some organism, bacterial or otherwise, was necessary to the development of duplication as here observed. If this

STOUT: FASCIATION IN CHICORY

should be the case it is evident that while the susceptibility is very decidedly limited to the variety it can be transmitted directly or indirectly though incompletely to large numbers of the offspring of a hybrid generation.

## Summary

An unusual type of fasciation occurs in the variety of chicory known as red-leaved Treviso. It consists of a very decided duplication in the main axis of the stem, giving two stem-elements with, however, a decided cohesion of the two. In this variety of chicory there are also various irregularities in the development of cotyledons and plumule. All degrees of fusion between the two cotyledons are in evidence; in some seedlings only one cotyledon is present. Occasionally no plumule develops.

The character of duplication and cohesion of the main axis is strongly but not completely heritable. There is wide variation in the degree of duplication and a few plants with a normal unduplicated main axis occur.

In an $F_1$ hybrid generation of crosses between plants with duplication and plants of wild stock which exhibit no tendency to such fasciation the character of duplication is incompletely dominant both as to degree of expression and number of plants affected. An intermediate type is strongly in evidence in which the only indication of duplication is seen in a mixed and irregular phyllotaxy.

## EXPLANATION OF PLATE XII

Nos. 1–9 inclusive are of stems of plants of the variety red-leaved Treviso; no. 7 is of the 1915 crop, all others are of the 1916 crop.

No. 1. Stem showing no duplication. Phyllotaxy regular.

No. 2. No duplication but stem thicker than in no. 1. Phyllotaxy regular.

No. 3. Stem of small plant. Short segment of duplication at *a*.

No. 4. Duplication from *a* to *b*; phyllotaxy above *a* is irregular with tendency for branches to be paired.

No. 5. Very decided duplication from *a* to *b*. Lesion separates the two stem-elements in lower center. Stem-elements parallel below but twisted above.

No. 6. Decided duplication with parts much twisted.

No. 7. The two stem-elements separate from the base. No lesions.

No. 8. Longitudinal lesions strongly developed. One stem-element much contorted.

No. 9. Much torsion with transverse lesion of one stem-element.

Nos. 10, 11 and 12 are $F_1$ hybrids of red-leaved Treviso × unfasciated plant of a wild variety.

No. 10. Duplication evident in lower two thirds of stem.

No. 11. Duplication indicated by a very slight but broad groove near base. Phyllotaxy mixed and irregular especially near base.

No. 12. No duplication. Phyllotaxy regular.

# A QUANTITATIVE STUDY OF RAUNKIAER'S GROWTH-FORMS AS ILLUSTRATED BY THE 400 COMMONEST SPECIES OF LONG ISLAND, N. Y.

NORMAN TAYLOR

*Brooklyn Botanic Garden*

The value of sorting species of plants into different categories, based on their growth-forms, has been pointed out so often that there scarcely seems further need of going over the subject again. The weakness of such a sorting and the percentages based on it, due to the fact that species, not individual plants, are considered, is obvious. Such percentages as have been published show not so much an actual response to climatic factors, as they do the multiplicity of forms that may have been developed. For most regions that is all that can be done, as anything like a plant census of a given region is usually impossible. Yet upon such a census, or some approximation to it, there could be based percentages of different growth-forms that reflect more accurately than any species percentage the actual climatic response of vegetation to climate.

The importance of getting, if possible, some growth-form percentages that should be quantitative rather than those based on species only resulted in a study of the flora of Long Island, N. Y., with this in view. The island is roughly 120 miles long and 12–16 miles wide and, excluding ferns and their allies, has about 1120 species of native plants. It is diversified as to vegetation, as there are good-sized areas of "scrub," mostly oak and Ericaceae, considerable deciduous forest, some extensive "pine-barrens," salt marshes, a small prairie, and the downs at Montauk and Shinnecock.

In a general study of the flora and vegetation of the island, distribution maps for each of the native species were made and have been posted up for several years. Such maps indicate actual collections represented by specimens in herbaria, field notes by the writer, all published records of species and descriptions of different vegetative areas by nearly all who have written about Long Island for the last 250 years. From Daniel Denton's History of New York, through the period when numerous Quaker journals were issued, down to the modern observations of professional botanists, these records have been accumulated. The opportunity, therefore, of getting something

like a comprehensive view of the flora and vegetation of the island is excellent.

Within the last few months it has been possible to separate the distribution maps of the species into two groups. The one which interests us just now is the smaller, consisting of the 400 commonest species. These make up the great bulk of the vegetation of the island, the other group of about 719 species being scattered and nothing like so common.

When these four hundred species are sorted into the different growth-form categories of Raunkiaer and their percentages reckoned, we find them grouped as follows:[1]

| Growth Form | Numbers of Species | Percentages of the Commonest Species |
|---|---|---|
| MG | 6 | 1.50 |
| MS | 12 | 3.00 |
| MC | 34 | 8.50 |
| N | 17 | 4.25 |
| CH | 29 | 7.25 |
| H | 120 | 30.00 |
| G | 84 | 21.00 |
| HH | 27 | 6.75 |
| T | 57 | 14.25 |
| Stem succulents | 8 | 2.00 |
| Parasites | 6 | 1.50 |

The amount of deviation from the normal spectrum of Raunkiaer or from the growth-form percentages of the total flora of Long Island, or from the percentages of the local flora area[2] should show an interesting relation. The figures are as follows:

| | MG | MS | MC | N | CH | H | G | HH | T |
|---|---|---|---|---|---|---|---|---|---|
| Normal spectrum | 6 | | 17 | 20 | 9 | 27 | 3 | 1 | 13 |
| Local flora | .52 | 4.03 | 7.18 | 3.51 | 5.29 | 33.29 | 20.23 | 11.74 | 13.00 |
| Total L. I. flora | .89 | 4.37 | 6.34 | 2.77 | 5.89 | 33.15 | 20.10 | 10.90 | 13.94 |
| 400 commonest Long Island species | 1.50 | 3.00 | 8.50 | 4.25 | 7.25 | 30.00 | 21.00 | 6.75 | 14.25 |

It will be seen from this table that the percentage of large and medium-sized trees, the herbs that root near the surface, and the annuals are somewhere near what the normal spectrum would lead one to expect. In fact the growth-form percentages of these 400 commonest Long Island species are in remarkable agreement with the percentages of the total Long Island flora and of that whole region

[1] Abbreviations for the different growth-forms are the same as those in general use. See Journ. Ecol. 1: 16–26. 1913 and Am. Journ. Bot. 2: 23–31. 1915.

[2] See Mem. N. Y. Bot. Gard. 5: 1–683. 1915 and Am. Journ. Bot. 2: 23–31. 1915. Stem succulents and parasites are omitted from now on as being too small to signify.

near New York which is here called the local flora. To all those who have wondered how much an actual plant census of any region would derange the Raunkiaer scheme, these figures will come as a surprise. It has been supposed by some that wherever there was a serious disparity between the growth-form percentages of a region and the normal spectrum, the fact that species, not individuals, were being considered was obscuring the truth.[3]

The fact that there is such a remarkable agreement between the percentages based on species and those based on frequency, and that both these sets of figures disagree radically from the normal spectrum, tends to increase the doubt as to the validity of the spectrum as laid down by Raunkiaer. In an earlier paper on the growth-forms of New York and vicinity, it was pointed out that "for no region in the world has there been published such a large percentage of these plants with bulbs, rhizomes, corms, and other subterranean methods of winter protection." Considering that 20.23 percent of geophytes in the local flora area should have occasioned this remark and that for the 400 commonest Long Island species, the figure is 21 percent, the case for the normal spectrum which calls for only 3 percent of these geophytes seems decidedly weak.

When it is remembered that in the normal spectrum our ordinary deep and shallow-rooted herbs call for only 30 percent, the aquatics 1 percent, and chamaephytes 9 percent, we have a total of only 40 percent for all herbaceous plants on the most favorable assumption. Actually many of the chamaephytes are low woody plants, so that the normal spectrum allows only about 35 percent for herbaceous plants of all kinds, excluding annuals, or 48 percent including them. The percentage for the same groups in the local flora area is about 79 percent, for all Long Island 83 percent, and for the 400 commonest species it is 78 percent. There can be here no question of the wrong assignment into the Raunkiaer growth from categories, for by lumping the chamaephytes (about half of which may be woody), hemicryptophytes, geophytes, aquatics, and annuals, we separate at once the woody from the herbaceous species. Does this difference of 30 percent in the herbaceous element of the vegetation of Long Island from that of the normal spectrum really mean that the region is so far off normal or that the normal spectrum itself is in need of further study?

It has been shown that there is a rather definite relation between the percentages of herbaceous and woody elements in temperate and tropical floras, but unfortunately the figures as published deal only with dicotyledons.[4] For our purposes, however, they show the per-

[3] Am. Journ. Bot. 2: 30. 1915.

[4] Sinnott, E. W., and Bailey, I. W. The origin and dispersal of herbaceous angiosperms. Ann. Bot. 28: 566–567. 1914.

centages of herbaceous plants based on the calculations of Sinnott and Bailey. Their table is as follows:

Temperate Regions

| Region | No of Species | No. of Herbs | Per Cent Herbs |
|---|---|---|---|
| Northeastern United States (Gray) | 2,280 | 1,748 | 77 |
| Northern United States (Britton and Brown) | 2,662 | 2,089 | 78 |
| Southeastern United States (Small) | 4,608 | 3,312 | 72 |
| Southern United States (Chapman) | 2,266 | 1,666 | 74 |
| Rocky Mountains (Coulter) | 2,206 | 1,910 | 87 |
| Los Angeles (Abrams) | 802 | 627 | 78 |
| Florida Keys (Small) | 415 | 225 | 54 |
| Great Britain (Hooker) | 927 | 821 | 89 |
| France (Cusin and Ansberque) | 3,924 | 3,492 | 89 |
| Germany (Engler) | 1,117 | 947 | 85 |
| Switzerland (Schinz and Keller) | 1,899 | 1,726 | 91 |
| Russian Empire (Ledebour) | 14,704 | 12,588 | 86 |
| Norway (Blytt) | 857 | 741 | 86 |
| Iceland (Stefansson) | 221 | 200 | 90 |
| Ellesmereland (Simmons) | 76 | 71 | 93 |
| Faroes (Warming et al.) | 164 | 150 | 91 |
| Spain (Ibiza) | 4,481 | 3,554 | 79 |
| Crete (Raulin) | 1,461 | 1,161 | 79 |
| Sicily (Tornabene) | 1,697 | 1,295 | 76 |
| Syria (Post) | 2,949 | 2,477 | 84 |
| Flora Orientalis (Boissier) | 9,771 | 8,110 | 83 |
| Japan (Matsumura) | 3,257 | 1,861 | 57 |

Tropical Regions

| | | | |
|---|---|---|---|
| Brazil (Mueller) | 15,981 | 4,092 | 26 |
| Ditto, Amazon Valley only | 2,209 | 265 | 12 |
| British West Indies (Grisebach) | 2,249 | 675 | 30 |
| Tropical Africa (Oliver and Thiselton-Dyer) | 8,577 | 3,560 | 42 |
| British India (Hooker) | 10,454 | 4,344 | 42 |
| Bombay (Cooke), Lowland only | 1,249 | 487 | 39 |
| Upper Gangetic Plain (Duthie) | 1,084 | 583 | 54 |
| Ceylon (Trimen) | 1,793 | 670 | 37 |
| Java (Koorders) | 3,188 | 867 | 27 |
| Dutch East Indies (Miquel) | 6,398 | 1,599 | 25 |
| Malay Peninsula (King) | 3,252 | 553 | 17 |
| Hongkong (Bentham) | 728 | 293 | 40 |
| Manila (Merrill) | 333 | 106 | 32 |

When it is remembered that these figures do not include monocotyledons they add additional weight to those given for the local flora area, the total Long Island Flora, and for the 400 commonest species on the island. Summarized these figures show the following percentages of herbs:

PERCENTAGES OF HERBS

| | | |
|---|---|---|
| 1. Normal spectrum, including all categories | 48% | |
| 2. Average of 15 North Temperate floras as listed above, excluding monocotyledons | 82% or about 90% | counting monocotyledons. |
| 3. Average of 13 Tropical floras as listed above, excluding monocotyledons | 31% or about 38% | counting monocotyledons. |
| 4. Australia[5] (excluding monocotyledons) | 30% or about 35% | counting monocotyledons. |
| 5. New Zealand[5] (excluding monocotyledons) | 55% or about 70% | counting monocotyledons. |
| 6. Local flora area, all categories | 79% | |
| 7. Total Long Island flora, all categories | 83% | |
| 8. **400 commonest Long Island species, all categories** | 78% | |

Items 2, 3, 4 and 5 do not count monocotyledons and a careful estimate of these monocotyledons shows that they make up form 1/5–1/3 of the floras of the regions mentioned. This monocotyledonous element is overwhelmingly herbaceous and it adds a great deal to the percentages of herbs in these items. Upon these figures the percentages, counting the monocotyledons, which are of course included in Raunkiaer's normal spectrum, are estimated as shown in the table above. The average of the percentages, including monocotyledons, in items 2, 3, 4 and 5 is 58 percent which is as near an estimate to the relation between herbaceous and woody species as we can get for the areas mentioned. These, with the exception of South America, make up the great bulk of the flora of the world and 58 percent of herbs as against 42 percent of woody plants can, for the present, be set down as a fair estimate. This is a clear 10 percent above the combined herbaceous percentages of Raunkiaer's normal spectrum, and very much nearer the percentages of the northern regions generally, where herbs predominate.

In other words, the evidence from large areas, based on species, and from a small area like Long Island, based on frequency of individuals, points unmistakably to the necessity of shifting some of the Raunkiaer growth-form percentages. Herbs make up the great majority of the vegetation in North Temperate regions, and, as we have seen, even in the tropics and southern hemisphere their bulk is by no means insignificant. Yet in the face of these figures, and of those of as complete a plant census of Long Island as we can get, the total herbaceous element according to Raunkiaer should be only 48 percent. As we have seen this is much too low for anything like a true vision of the relation between herbs and woody plants in the whole North Temperate region, and it is 10 percent lower than the

[5] Ann. Bot., *l. c.*, p. 583, 585.

figure for nearly the whole world. This is the chief point made here. For, if the percentages of woody and herbaceous species, as shown by Sinnott and Bailey, and percentages based on an approximation to a plant census as shown by the figures from Long Island are not in substantial agreement with Raunkiaer's system, then it follows that that system does not, as yet, show what has been claimed for it. Just what reshifting of the percentages in the normal spectrum is necessary lies outside the scope of this paper. It seems evident, however, that they need more study and over large areas, preferably based on plant censuses such as has been attempted on Long Island. With the completion of such studies we might have in the revised percentages more accurate data as to climatic response than is possible at present.

# THE ANCIENT OAKS OF AMERICA

WILLIAM TRELEASE

*University of Illinois*

While studying the oaks which are now so striking a component of the vegetation of North America, I have found it necessary to form some idea of the history of *Quercus* before our own day. Neither time nor opportunity has offered for basing this on a reexamination of the scattered materials that have served for the classic studies of Lesquereux and Newberry, or for the later work of Hollick, Knowlton, Berry and Cockerell; but from a careful examination of descriptions and illustrations I have tried to bring into some sort of orderly assemblage the scattered facts that have been observed and described (1).

So far as I know, only two of our fossil species (*Q. consimilis* and *Q. paucidentata*, both of the Eocene) are known in fruit (2); the others, though exceptionally with twig remnants, are represented usually by dissociated leaves, sometimes well preserved but frequently only in fragments showing little detail. These materials have been referred to *Quercus* because of the general appearance and especially the venation of the leaves when this is ascertainable. It is not surprising that misapprehension should have existed occasionally as to the age of clay and similar deposits in which some have been found, or that some of them should have been transferred to genera of other families, even, as a result of further study; indeed a considerable number of these fossils appear to have been called oaks rather because they could be called nothing else than for any very positive other reason (3).

When the American fossils were first studied, the genus *Quercus* was made to include a number of forms that are segregated now in the genus *Dryophyllum* (4), held to be prototypic of the family Fagaceae rather than of its dominant genus, *Quercus*. The natural early tendency, as would be expected of conservative and experienced botanists working with isolated and fragmentary leaves, was to stretch the limits of species so as to recognize identities of Old and New World species, rather than to see dependable differences in such a representation, especially in a genus recognized as unusually variable in the foliage of even individual trees of existing species. None of the recently described species has been identified with a European form, and most of the earlier identities have been discarded, sometimes by

those who had believed in them at first (5). At present, only the following identities with European species stand, and these, apparently, because their representations have not been reexamined: CRETACEOUS—*Q. hieracifolia* (Kas.), *Q. straminea* (Col.); EOCENE—*Q. Chamissonis* (Alaska), *Q. doljensis* (Wyom.), *Q. drymeja* (Oreg.), *Q. eucalyptifolia* (Col., N. Mex., Miss.), *Q. Godeti* (Mont.); MIOCENE—*Q. elaena* (Col.), *Q. Steenstrupi* (Calif.). One European species, *Q. Gaudini*, very indefinitely reported as American, seems to have no ascertainable significance.

Unfortunately until recent years nomenclature has been treated independently in the several branches of natural history, even in different groups of the same kingdom. Under this uncorrelated procedure, fossil and existing species have been independently named, with the result that a given name may refer sometimes to the former and sometimes to the latter although no idea of identity or even relationship within the genus has been intended in their designation. No procedure appears sensible except the restriction of a given binomial to a single species, and the acceptance of such a name as valid from its earliest publication, whether for a fossil or extant species. Application of this procedure causes a considerable number of changes among the names of American fossil oaks, as well as among species that are now living (6).

On this continent, as in the Old World, the earliest appearance of *Quercus* is in the Cretaceous, for which 48 nominal species are known from scattered deposits in the Atlantic States of New York, New Jersey, Maryland, North Carolina and South Carolina; in Kansas and Nebraska in the Plains region; in Wyoming, Montana, Colorado and New Mexico in the Rocky Mountains; in Utah in the Great Basin; and, quite isolated, in Vancouver in the northwest. None of these species is known to have survived Cretaceous time, and none bears striking resemblance to any existing oak, though holly-like leaves were found then as now.

For the Eocene, 56 nominal species are reported from scattered deposits in Canada and (perhaps questionably) Mississippi in the east; from North Dakota, Wyoming, Montana, Colorado and New Mexico in the interior; and from Oregon, Washington and Alaska in the northwest. No species is known to have survived into the Miocene, and none appears to be related to existing species, though holly-like leaves are represented among these fossils.

The nominal species for the Miocene number 42 and they have been found in scattered deposits from Maryland, the District of Columbia and Virginia in the east; and from Colorado, Montana, Idaho, Oregon, California and Nevada in the west. One of these

Miocene oaks, of California, has been held to be varietally related to the existing golden oak of California, and is known as *Quercus chrysolepis montana;* but little can be said for or against this reputed relationship. Except for this, none of the Miocene oaks is thought to have survived.

Little is known of the Pliocene in North America, and it may be that the sparing deposits in Maryland and Alabama that are supposed to be of this horizon may be open to some question whether they are not of more recent age. The 4 nominal species of *Quercus* that have been found in them are distinctly more like modern oaks than anything that preceded, but identities with existing species are not clearly evident to me (7). In South America, several fossil oaks from the Pliocene have been described, not evidently related to existing oaks, from localities far from any existing species (8). At present only four oaks occur in South America; these, which grow in the interior mountains of Colombia, form a natural group which appears more closely related to some of the Costa Rican oaks than to any others that are now known (9).

If the term Pleistocene be used to designate glacial or later deposits in which fossils are found, it is to be assumed that these fossils will be very similar to if not identical with existing species. Scattered deposits of this kind have been examined from various points in the Atlantic region—Canada, New Jersey, Pennsylvania, Maryland, Virginia and Kentucky; and from California in the Pacific region. From these deposits 20 oaks have been named. Two of them, *Q. predigitata* Berry and *Q. pseudo-alba* Hollick, are separately designated as the ancestral forms respectively of *Q. digitata* or *falcata* and *Q. alba*, both of which are held to be represented by other Pleistocene material. A third, *Q. abnormalis* Berry, may have been a teratological bifid form of *Q. Phellos*, which is known in its normal form from Pleistocene deposits. Concerning a fourth species, *Q. Glennii* Hollick, I must admit a serious doubt as to the horizon to which it is ascribed. The remaining 16 species, into which I have merged *Q. abnormalis*, *Q. predigitata* and *Q. pseudo-alba*, are easily identified with species now living in the regions in which they have been found fossilized and, as would be supposed from this, all of these Pleistocene oaks are from the Atlantic region, except *Q. chrysolepis*, which was collected in California.

Even a cursory inspection of the many illustrations of fossil oaks that have been published shows that collectively or for any given period they present a multiplicity of leaf forms more or less comparable with what is known for existing species; indeed Professor Cockerell, who has given much attention to the point, finds in *Quercus*

a good illustration of an ample but inherently limited range of variation within which in the passage of long periods of time the same general cycle of forms has appeared repeatedly.

It has seemed to me worth while to arrange the principal leaf types of the Cretaceous and Tertiary fossils comparatively without regard to horizon; and for convenience of reference rather than as implying relationships, those of general comparability are brought together by the following key:

| | |
|---|---|
| Leaves entire. | |
| Oblanceolate-obovate, large. (Pl. XIII.) | MAGNIFOLIAE. |
| Lanceolate or oblong, moderate. (Pl. XIV.) | SIMULATAE. |
| Leaves toothed. | |
| Teeth numerous, small and sharp. | |
| Leaves elongated, moderate. (Pl. XV.) | FRAXINIFOLIAE. |
| Leaves short and broad, small. (Pl. XXII.) | SPURIO-ILICES. |
| Teeth sparse or coarse. | |
| Leaves broad, moderate. (Pl. XVI.) | DISTINCTAE. |
| Leaves elongated. | |
| Rather large, not pointed. (Pl. XIX.) | CASTANEOPSES. |
| Moderate, acuminate. (Pl. XIX, XX.) | PAUCIDENTATAE. |
| Small, not pointed. (Pl. XXII.) | SPURIC-ILICES. |
| Leaves crenate or repand. | |
| Rather elongated and small. (Pl. XXII.) | MYRICAEFOLIAE. |
| Broad, moderate. | |
| Some teeth acute. (Pl. XVIII.) | SUSPECTAE. |
| Teeth all rounded. (Pl. XVII.) | DALLIEAE. |
| Leaves incised or lobed. | |
| Lobes or shoulders 2 or 3, toward the apex. (Pl. XXII.) | BICORNES. |
| Lobes or divisions several, not apical. | |
| Leaves small, few-lobed. (Pl. XXI.) | LAMBERTENSES. |
| Leaves moderate or large. (Pl. XXI.) | LOBATAE. |

These foliage-groups scarcely appear to me comparable with existing oaks except for the Magnifoliae, which suggest certain large-leaved white oaks of Mexico and Central America; the Simulatae, which may be held to resemble more or less closely some of the entire-leaved black and white oaks of the United States and tropical America; the Spurio-ilices, which parallel the holly-leaved black oaks of California, and white oaks like *Q. Douglasii*, many of the scrub oaks of the table-land, and the dwarf live oaks of the Gulf States; the Paucidentatae and Castaneopses, somewhat suggestive of existing white oaks with chestnut-like foliage; some of the Lobatae, comparable with the white oaks of the United States which have lobed foliage, as well as with some of the existing chestnut oaks; and the Lambertenses, which resemble if they differ from existing black oaks. Of the lobed forms, one only, *Q. ursina*, apart from these, at all recalls our familiar incised black-oak foliage to my eye.

The groups which find no existing parallel in the genus may be questioned as really representative of *Quercus*. The Fraxinifoliæ are not known since early Tertiary time, but they constituted about 11 percent of American Cretaceous species referred to this genus, and about 17 percent in the Eocene. The Distinctae formed about 15 percent through the Cretaceous, Eocene and Miocene, with changing species. The Suspectae constituted about 20 percent of the whole in the Cretaceous, but only about 10 percent in the Eocene, and they fell to some 4 percent in the Miocene. Neither of the groups that I have called Myricaefoliae and Bicornes is known to have had more than a small and transient representation—*Q. praeundulata* in the Cretaceous and *Q. Ramaleyi* in the Miocene for the former, and *Q. bicornis* and *Q. negundoides* in the Eocene for the latter; and the Dallieae are represented only by *Q. Dallii* of the Eocene.

The ancient foliage types more or less comparable with those of today show the following relative abundance at different times, so far as records go: The chestnut type, now most largely represented, with nearly half the existing American species, formed one tenth of the whole in the Cretaceous, over a third in the Eocene, and about one seventh in the Miocene: over a fourth of the known Pleistocene oaks have this kind of foliage. About 16 percent of the known living American oaks have lobed leaves, and nearly half of those known from the Pleistocene are of this general kind; though about a third of those known for the Miocene are of this type, none of them has bristle-tipped lobes so far as I know; and in the Eocene only about 3 percent are found to have had lobed leaves. The pungent or holly-like type, now constituting about 4 percent of the whole and represented by one form in the Pleistocene, contained about 15 percent of the Miocene and 9 percent of the Cretaceous forms, though it is not yet recognized in Eocene deposits. As might, perhaps, be expected, entire-leaved oaks, now represented by over a third of the known species, have been abundant throughout the history of the genus, and nearly a third of the Cretaceous, a fifth of the Eocene, and a fourth of the Miocene and of the Pleistocene, species possessed this type of foliage, which today is often found associated with holly-like or comparably toothed leaves, often in the same species or even on the same individual.

It does not seem profitable to attempt to draw climatic inferences from what I can see in these fossil oak leaves. Some of the entire leaves appear to have been rather coriaceous, as in certain semi-xerophytic species now living on the Mexican table-land, and these and the holly-leaved forms may have been somewhat xerophytic. Most of the leaves look as if they might have belonged to mesophytes.

One group only, the Paucidentatae, even remotely suggests a rain-tip in its acumination, but the Eocene *bicornis* and *negundoides* are somewhat pointed, and some of the more deeply divided forms have acute lobes, though these do not appear to have been more than mucronate.

One of the characters largely relied on by palaeobotanists is the venation of leaves. The significance of this has been insisted on by Oersted (10) and especially by von Ettingshausen, in the discussion of *Quercus*. Some years before his death, this distinguished Austrian botanist published an extensive tabular comparison of the venation of existing American oaks and (chiefly European) fossils ascribed to the same genus (11). For one interested in the Old World fossils, the table should be most instructive, since it often brings into association a number of fossil species through comparison with a single living one. On the other hand, the assembling of several existing species through comparison with a single fossil is suggestive of resemblances which might escape notice otherwise and which may indicate some sort of relationship between them.

As a general thing, these venation associations corroborate conclusions of affinity based on other considerations, as for instance *Q. macrocarpa**[1] and *stellata** in comparison with *Q. Buchii; Q. digitata*†, *Kelloggii*†, × *Leana*† and *rubra*† in comparison with *Q. cruciata;* and *Q. Douglasii** and *stellata** in comparison with *Q. cymaena* (12).

It is interesting to see that *Q. virginiana** is brought into comparison with *Phellos*† under *Q. elaena*, and with *imbricaria*† under *Q. chlorophylla*, for even good botanists have found difficulty in distinguishing between the leaves of some of our Southern live oaks and the black oaks with willow- or myrtle-like foliage.

Less fortunate associations appear to be those in which unrelated species are thus brought together; *e. g.*, *Q. marilandica*† and *Warscewiczii** through *Q. Zoroastri; Q. magnoliaefolia** and *nigra*† through *Q. sinuatiloba; Q. Garryana** and *ilicifolia*† through *Q. liriodendroides; Q. undulata** and *Wislizeni*† through *Q. firma;* and, especially, *Q. chrysolepis*,‡ *grisea*,* *lanceolata*† and *laurina*† through *Q. lauriformis.*

Though not necessarily the most abundant at any period, or the most typical in the Fagaceae, the most synthetic of the many leaf-forms shown by past and present oaks appears to me to be the subpungent or holly-like type. Those who are familiar with the existing Californian oaks know with what ease toothing passes into the entire margin in *Q. chrysolepis* and its allies, and into the lobed outline in *Q. Douglasii;* and it is very frequent in juvenile forms.

Engelmann's confidence in foliage characters was shaken by the

[1] In this comparison, species of *Leucobalanus* are indicated by *, those of *Erythrobalanus* by †, and those of the intermediate *Protobalanus* by ‡.

existing *Q. undulata*, as he understood that species, in which were comprised entire, frequently toothed, and very deeply lobed forms, some of which he was disposed to segregate varietally as others have done specifically, but all intergrading, as he saw it, as forms of one single extremely polymorphic species (13).

Similar polymorphism is shown by the many forms of associated European Tertiary oak leaves studied by von Ettingshausen and included in his conception of *Q. palaeo-ilex*. Guided by venation studies, he was able to see in this species a foreshadowing of all of the modern types of oak foliage (14). In the absence of other knowledge than we now possess, I am disposed to think that in the holly-like form we may see a starting point for the successive reevolution of the various forms of leaf that *Quercus* has presented in the several geological ages, and now presents.

## References

1. An indispensable aid in locating first references to American post-carboniferous fossil plants, in this as in other genera, is Professor Knowlton's catalogue of Cretaceous and Tertiary plants, published as Bulletin no. 152 of the United States Geological Survey—though it is now antiquated.

2. Fruit of *Q. consimilis* and *Q. paucidentata* is figured by Hollick in Monograph 35 of the U. S. Geological Survey, Pl. 43.

3. Nominal species of *Quercus* subsequently transferred to other families than Fagaceae are *Q. anceps* Lesq. (*Diospyros ambigua*), *Q. Benzoin* Lesq. (*Persea Leconteana*), *Q. californica* Lesq. (*Mespilodaphne pseudoglauca*), *Q. chlorophylloides* Knowlt. (*Pisonia chlorophylloides*), *Q. elkoana* Lesq. (*Carpinus grandis*), *Q. Lyellii* Lesq. (*Nectandra lancifolia*), *Q. microdentata* Hollick (*Dillenites microdentatus*), *Q. Mudgii* Lesq. (*Protophyllum Mudgii*), *Q. myrtifolia* Lesq. (*Sophora Lesquereuxii*), *Q. platania* Lesq. (*Platanus cordata*), *Q. retracta* Lesq. (*Myrica bentonensis*), *Q. Saffordi* Lesq. (*Banksia Saffordi*), *Q. semialata* Lesq. (*Anisophyllum semialatum*).

4. Nominal North American species of *Quercus* subsequently transferred to *Dryophyllum* are *Q. crassinervis* Lesq. (*D. tennesseense*), *Q. gracilis* Newb. (*D. subfalcatum*), *Q. Moorii* Lesq. (*D. Moorii*).

5. The following European fossil species of *Quercus* are now believed to be represented by segregable American forms: *Q. acrodon* (*Q. Lesquereuxiana* Knowlt.), *Q. angustiloba* (*Q. prae-angustiloba* Knowlt.), *Q. chlorophylla* (*Q. chlorophylloides* Knowlt.), *Q. furcinervis* (*Q. furcinervis americana* Knowlt.), *Q. Johnstrupii* (*Q. raritanensis* Berry), *Q. Laharpi* (*Q. fraxinifolia* Lesq.), *Q. mediterranea* (*Q. peritula* Cock.), *Q. pyrifolia* (*Q. florissantensis* Cock.), *Q. voyana* (*Q. distincta* Lesq.).

6. The following American fossil oaks require renaming because their names are preoccupied in the genus: *Q. affinis* Knowlt., not Scheidw. (**Q. clarnensis** n. nom.), *Q. Breweri* Lesq., not Wats. (**Q. Berryi** n. nom.), *Q. cuneata* Newb., not Wang. (**Q. Newberryi** n. nom.), *Q. elliptica* Newb., not Née (**Q. washingtonensis** n. nom.), *Q. latifolia* Lesq., not Steud. (**Q. dryophyllopsis** n. nom.), *Q. laurifolia* Newb., not Michx. (**Q. Penhallowi** n. nom.), *Q. montana* Knowlt., not Willd. (**Q. Cockerellii** n. nom.), *Q. occidentalis* Knowlt., not Gay (**Q. vancouveriana** n. nom.), *Q. pandurata* Heer, not H. & B. (**Q. alaskana** n. nom.), *Q. salicifolia* Newb., not Née (**Q. Eamesi** n. nom.), *Q. sinuata* Newb., not Walt. (**Q. prae-undulata** n. nom.), *Q. Turneri* Knowlt., not Willd. (**Q. prae-dumosa** n. nom.).

7. North American oaks ascribed to the Pliocene are *Q. catesbaeifolia* Berry, *Q. lambertensis* Berry, *Q. nigra* L. fide Berry, *Q. prae-virginiana* Berry. See Berry, Professional Paper no. 98L, U. S. Geol. Surv., p. 200.

8. Brazilian Pliocene oaks are *Q. brasiliensis* Krass., *Q. Hussakii* Krass., *Q. prae-mespilifolia* Krass., *Q. pseudodaphnes* Krass. See Krasser, Sitzungsber. K. Akad. Wien. **112**[1]: 854.

9. A summary analysis of existing American oaks is given by the writer in Proc. Nat. Acad. Sci. **2**: 626–9.

10. Oersted, Bidrag til Kundskab om Egefamilien i Nutid og Fortid (Vidensk. Selsk. Skr. Naturvid.-math. Afd. 5 ser. **6**: 335), Copenhagen, 1871: Chênes de l' Amérique Trop., p. 6.

11. Von Ettingshausen, Denkschr. K. Akad. Wien. Mathemat.-Naturwiss. Classe. **63**: 126. This discussion stands in relation with a series of three largely illustrated "Beiträge zur Erforschung der atavistischen Formen an lebenden Pflanzen und ihrer Beziehungen zu den arten ihrer Gattung" (*op. cit.* **54**: 245–254; **55**: 1–38; **56**: 47–68), published jointly with Krašan.

12. The following names of European fossil oaks employed in von Ettingshausen's comparison tables are preoccupied in the genus: *Q. affinis* Sap., not Scheidw. (**Q. paramoea** n. nom.), *Q. crassipes* Heer, not H. & B. (**Q. pachypoda** n. nom.), *Q. undulata* Web., not Torr. (**Q. cymaena** n. nom.).

13. Engelmann, Trans. Acad. St. Louis **3**: 372; Bot. Works. 389.

14. Von Ettingshausen, *l. c.* 125.

## EXPLANATION OF PLATES XIII–XXII

PLATE XIII. MAGNIFOLIAE.—CRETACEOUS: 1. *Q. Wardiana.* Lesquereux, Monog. U. S. Geol. Surv. **17**. pl. 7.—EOCENE: 2. *Q. magnifolia.* Knowlton, Monog. U. S. Geol. Surv. **32**. pl. 88.

PLATE XIV. SIMULATAE.—CRETACEOUS: 1. *Q. montanensis.* Knowlton, Bull. U. S. Geol. Surv. 163. pl. 1. 2. *Q. coriacea.* Hollick, Monog. U. S. Geol. Surv. **35**. pl. 19. 3. *Q. Eamesi*, n. nom. Hollick, Monog. U. S. Geol. Surv. **35**. pl. 1 (as *Q. salicifolia* Newberry, a preoccupied name). 4. *Q. glascoena.* Lesquereux, Monog. U. S. Geol. Surv. **17**. pl. 6. 5. *Q. Morrisoniana.* Lesquereux, Rep. U. S. Geol. Surv. **8**. pl. 17.—EOCENE: 6. *Q. neriifolia.* Lesquereux, Rep. U. S. Geol. Surv. **8**. pl. 31.—MIOCENE: 7. *Q. convexa.* Lesquereux, Rep. U. S. Geol. Surv. **8**. pl. 45 B. 8. *Q. dayana.* Knowlton, Bull. U. S. Geol. Surv. 204. pl. 6. 9. *Q. simulata.* Knowlton, Rep. U. S. Geol. Surv. $18^3$. pl. 101. 10. *Q. elaena.* Lesquereux, Rep. U. S. Geol. Surv. **8**. pl. 28.—HORISON?: 11. *Q. cinereoides.* Lesquereux, Rep. U. S. Geol. Surv. **7**. pl. 21.

PLATE XV. FRAXINIFOLIAE.—CRETACEOUS: 1. *Q. flexuosa.* Hollick, Monog. U. S. Geol. Surv. **35**. pl. 19. 2. *Q. banksiaefolia.* Hollick, Mon. U. S. Geol. Surv. **35**. pl. 18. 3. *Q. Holmesii.* Lesquereux, Rep. U. S. Geol. Surv. **1874**. pl. 8 (as *Q. salicifolia*).—EOCENE: 4. *Q. fraxinifolia.* Lesquereux, Rep. U. S. Geol. Surv. **7**. pl. 20. 5. *Q. Haidingeri.* Lesquereux, Rep. U. S. Geol. Surv. **7**. pl. 20. 6. *Q. consimilis.* Hollick, Monog. U. S. Geol. Surv. **35**. pl. 43. 7. *Q. drymeja.* Lesquereux, Rep. U. S. Geol. Surv. **7**. pl. 19; **8**. pl. 54. 8. *Q. Crossii.* Lesquereux, Proc. U. S. Nat. Mus. **10**. pl. 2.

PLATE XVI. DISTINCTAE.—CRETACEOUS: 1. *Q. alnoides.* Lesquereux, Monog. U. S. Geol. Surv. **17**. pl. 7. 2. *Q. Lesquereuxiana.* Lesquereux, Rep. U. S. Geol. Surv. **7**. pl. 19 (as *Q. acrodon*).—EOCENE: 3. *Q. viburnifolia.* Lesquereux, Rep. U. S. Geol. Surv. **7**. pl. 20.—MIOCENE: 4. *Q. distincta.* Lesquereux, Mem. Mus. Comp. Zool. $6^2$. pl. 2.—UNPLACED TERTIARY: 5. *Q. aquamara.* Ward, Bull. U. S. Geol. Surv. **37**. pl. 2. 6. *Q. carbonensis.* Ward, Bull. U. S. Geol. Surv. **37**. pl. 9.

PLATE XVII. DALLIEAE.—EOCENE: *Q. Dallii.* Lesquereux, Proc. U. S. Nat. Mus. **5**. pl. 8.

PLATE XVIII. SUSPECTAE.—CRETACEOUS: 1. *Q. suspecta.* Lesquereux, Monog. U. S. Geol. Surv. **17**. pl. 47. 2. *Q. dryophyllopsis* n. nom. Lesquereux, Rep. U. S. Geol. Surv. **1874**. pl. 6 (as *Q. latifolia*, a preoccupied name). 3. *Q. Cockerellii* n. nom. Knowlton, Bull. U. S. Geol. Surv. 257. pl. 17 (as *Q. montana*, a preoccupied name).—EOCENE: 4. *Q. pseudo-alnus.* Lesquereux, Rep. U. S. Geol. Surv. **8**. pl. 53. 5. *Q. Culveri.* Knowlton, Monog. U. S. Geol. Surv. $32^2$. pl. 87.

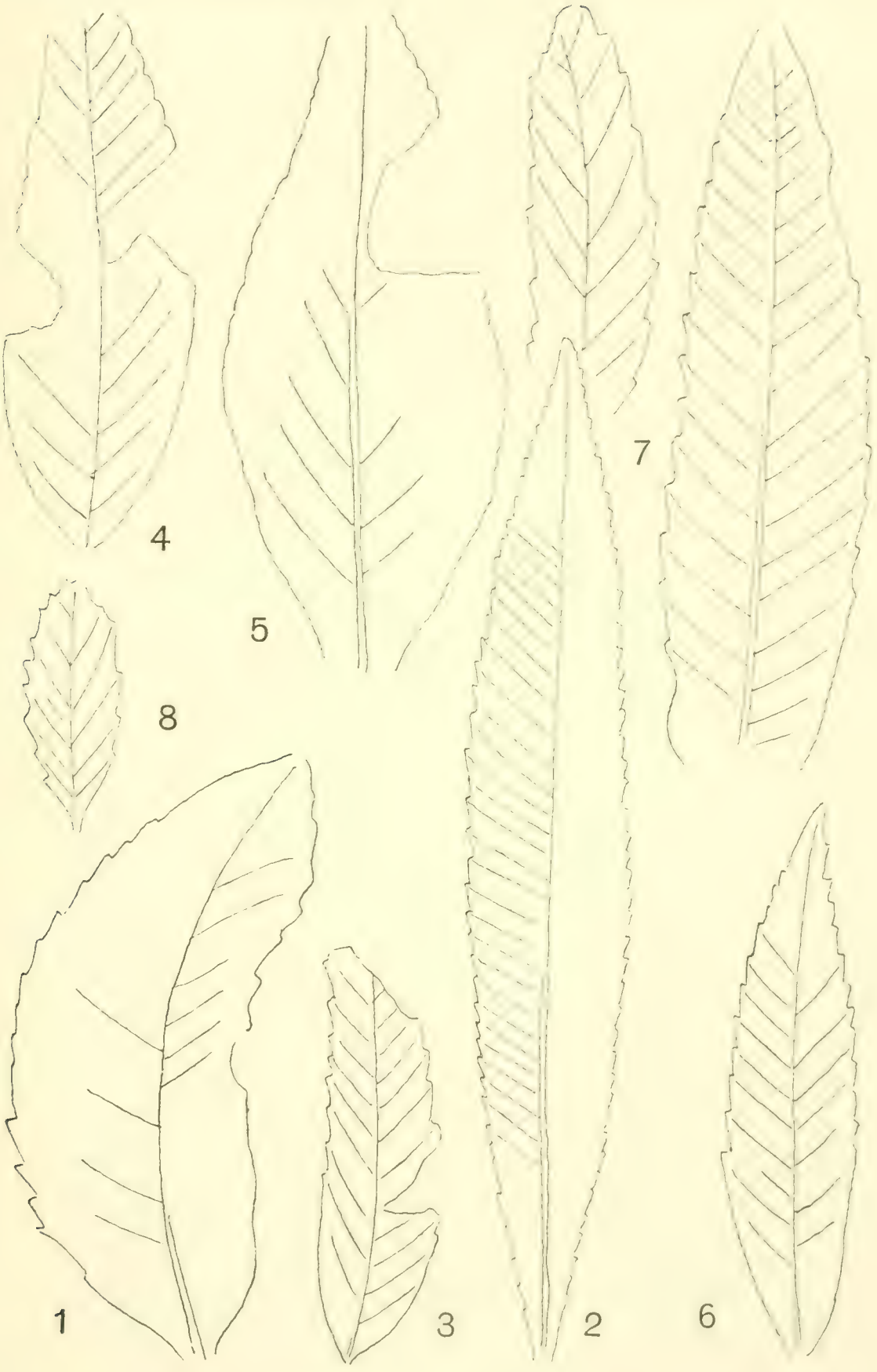
PLATE XIX. CASTANEOPSES.—EOCENE: 1. *Q. castaneopsis.* Lesquereux, Rep. U. S. Geol. Surv. **8**. pl. 28. 2. *Q. groenlandica.* Hollick, Monog. U. S. Geol. Surv. **35**. pl. 54.—PAUCIDENTATAE.—EOCENE: 3. *Q. clarnensis.* Lesquereux, Rep. U. S. Geol. Surv. **8**. pl. 53. (as *Q. furcinervis*).—4. *Q. nevadensis.* Lesquereux, Mem. Mus. Comp. Zool. $6^2$. pl. 2.

PLATE XX. PAUCIDENTATAE.—EOCENE: 1. *Q. yanceyi.* Knowlton, Monog. U. S. Geol. Surv. $32^2$. pl. 89. 2. *Q. paucidentata.* Hollick, Monog. U. S. Geol. Surv. **35**. pl. 43. 3. *Q. pseudo-castanea.* Unger, Palaeontographica. **2**. pl. 35.—MIOCENE: 4. *Q. Osbornii.* Lesquereux, Rep. U. S. Geol. Surv. **8**. pl. 38.

PLATE XXI. LOBATAE.—MIOCENE: 1. *Q. Merriami.* Knowlton, Bull. U. S. Geol. Surv. 204. pl. 6. 2. *Q. pseudo-lyrata.* Lesquereux, Mem. Mus. Comp. Zool. $6^2$. pl. 2. 3. *Q. Milleri.* Berry, Journ. Geol. **17**: 24. f. 3. 4. *Q. duriuscula.* Knowlton, Bull. U. S. Geol. Surv. 204. pl. 8.—LAMBERTENSES.—MIOCENE: 6. *Q. chapmani-*

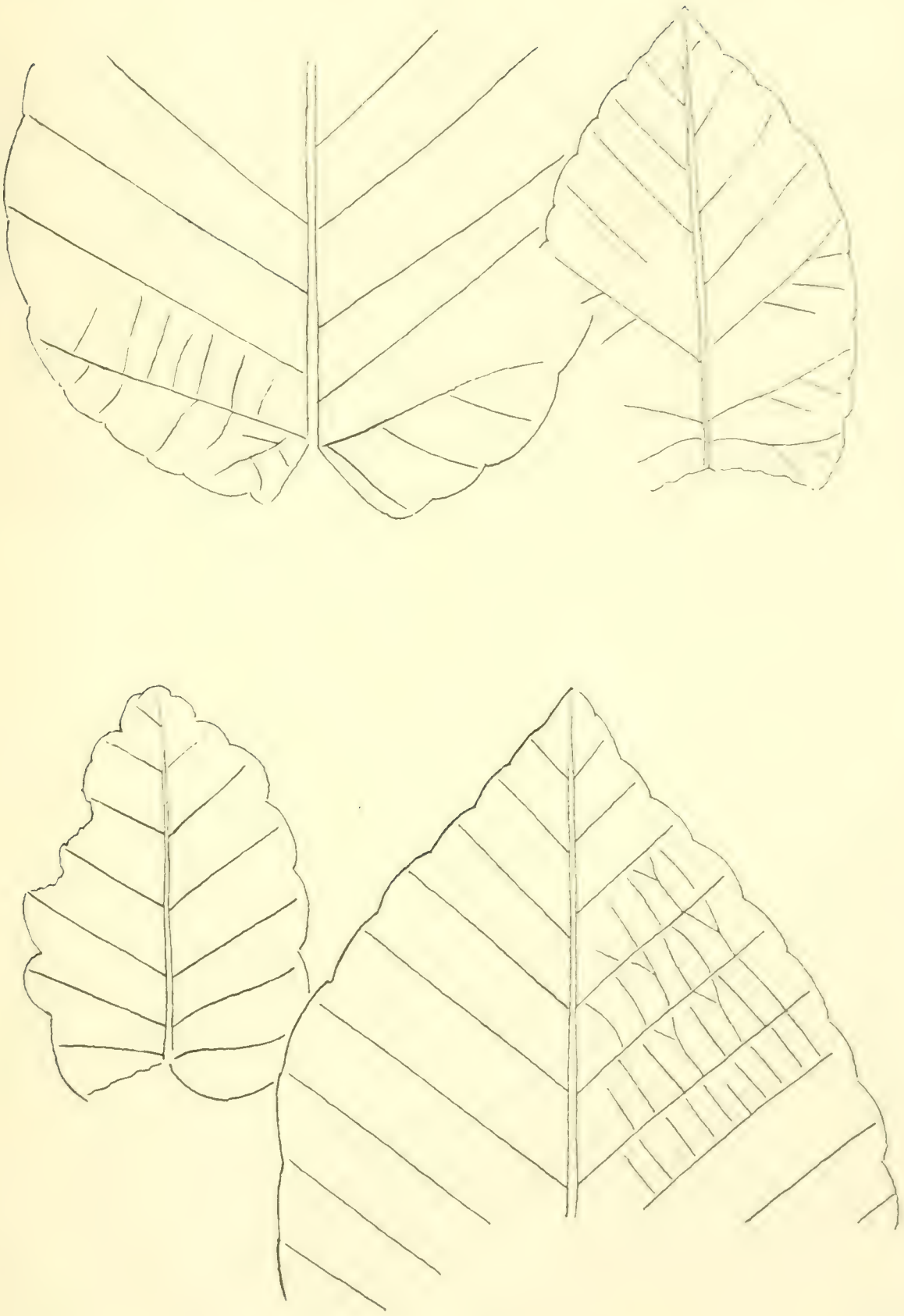
TRELEASE: QUERCUS — MAGNIFOLIAE

TRELEASE: QUERCUS — SIMULATAE

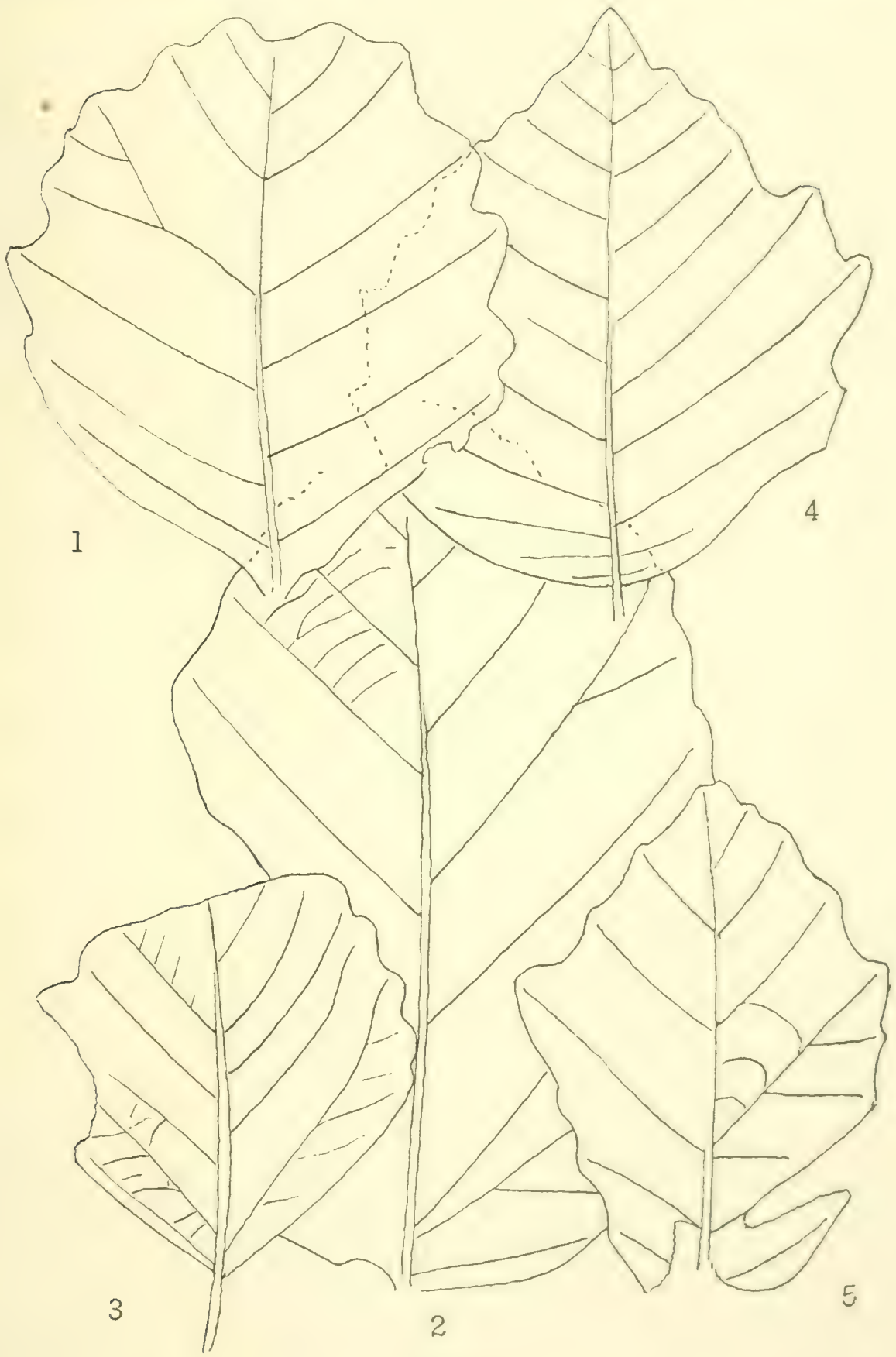



TRELEASE: QUERCUS — FRAXINIFOLIAE

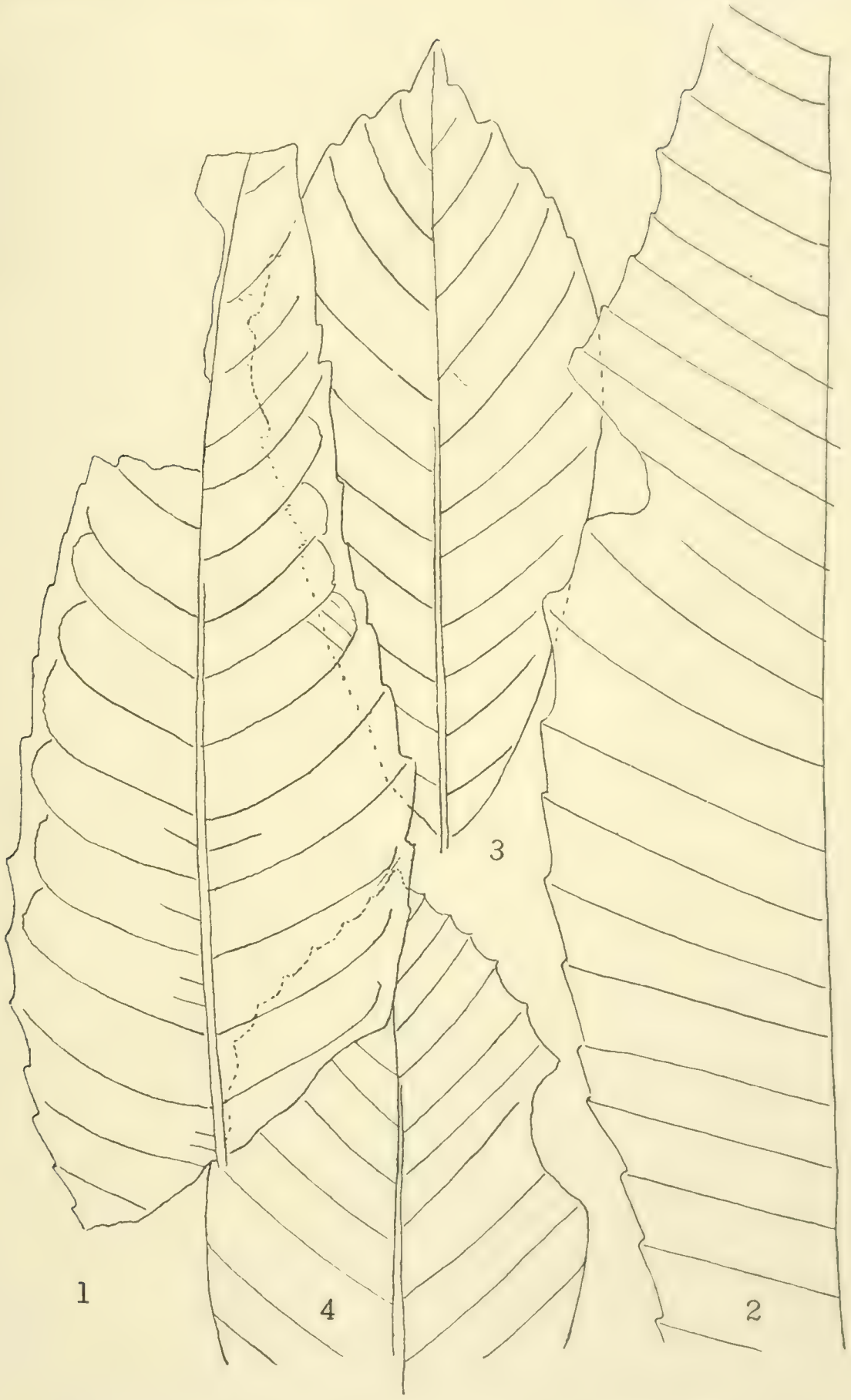
TRELEASE: QUERCUS — DISTINCTAE



TRELEASE: QUERCUS — DALLIEAE



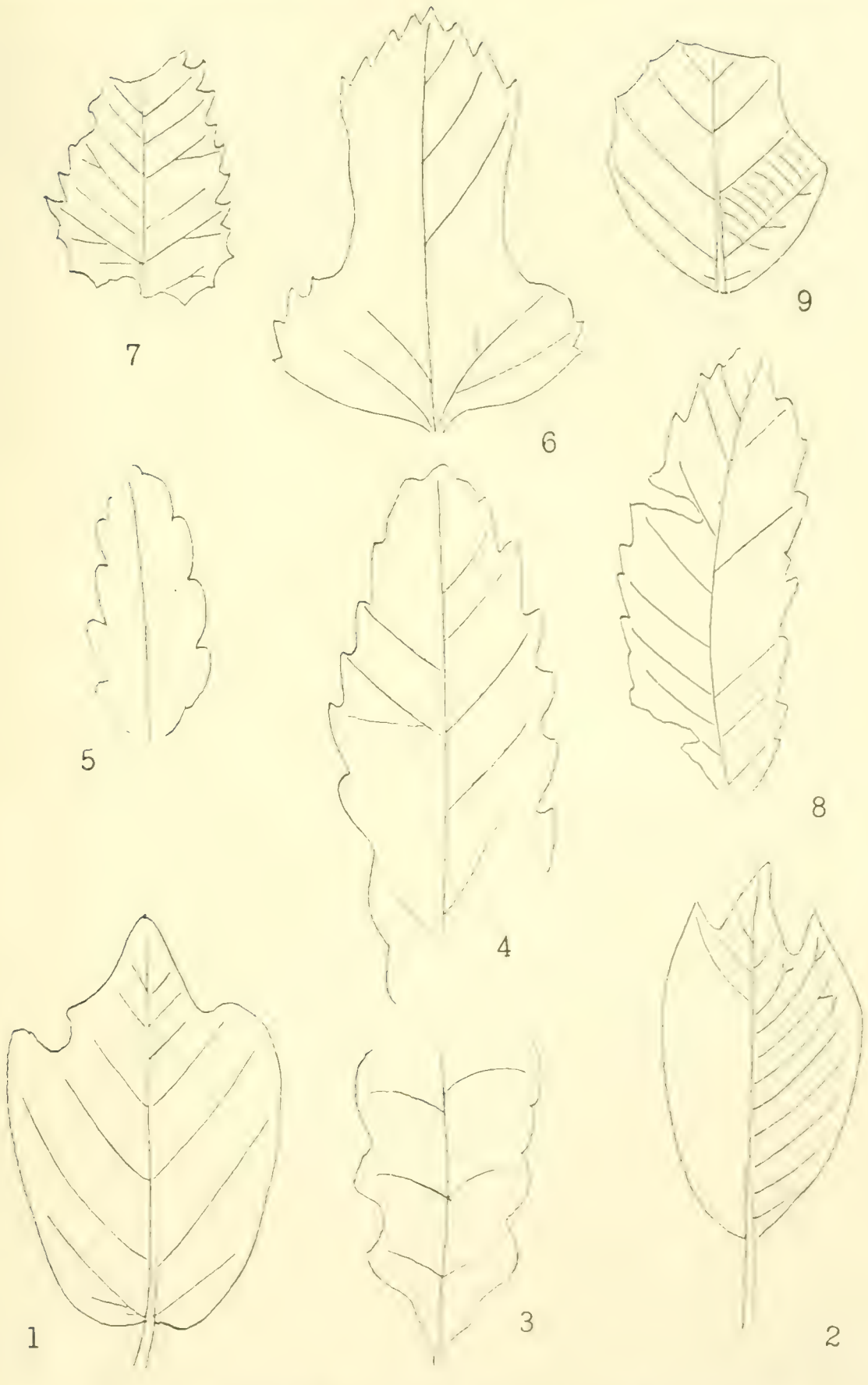

TRELEASE: QUERCUS — SUSPECTAE




TRELEASE: QUERCUS — CASTANEOPSES, PAUCIDENTATAE

TRELEASE: QUERCUS – PALUDENTATAE

TRELEASE: QUERCUS — LOBATAE, LAMBERTIENSES




TRELEASE: QUERCUS — BICORNES, MYRICAEFOLIAE, SUBRIC-ILICES

*folia*. Berry, Prof. Paper U. S. Geol. Surv. 98L. pl. 11. 7. *Q. Lehmanni*. Hollick, Md. Geol. Surv. Miocene. pl. 483.—PLIOCENE: 8. *Q. lambertensis*. Berry, Prof. Paper U. S. Geol. Surv. 98L. pl. 11.

PLATE XXII. BICORNES.—EOCENE: 1. *Q. negundoides*. Lesquereux, Rep. U. S. Geol. Surv. 7. pl. 21. 2. *Q. bicornis*. Ward, Bull. U. S. Geol. Surv. 37. pl. 9.—MYRICAEFOLIAE.—CRETACEOUS: 3. *Q. praeundulata*. Hollick, Monog. U. S. Geol. Surv. 35. pl. 31 (as *Q. sinuata* Newb., a preoccupied name). 4. *Q. antiqua*. Hollick, Monog. U. S. Geol. Surv. 35. pl. 13.—MIOCENE: 5. *Q. Ramaleyi*. Cockerell, Bull. Torr. Bot. Cl. 33: 309.—SPURIC-ILICES.—CRETACEOUS: 6. *Q. Haydeni*. Lesquereux, Rep. U. S. Geol. Surv. 7. pl. 19. 7. *Q. spuric-ilex*. Knowlton, Monog. U. S. Geol. Surv. 17. pl. 48.—MIOCENE: 8. *Q. Applegatei*. Knowlton, Rep. U. S. Geol. Surv. $20^3$. pl. 1. 9. *Q. distincta*. Lesquereux, Mem. Mus Comp. Zool. $6^2$. pl. 2 (as *Q. voyana*).

# THE ABSORPTION OF CALCIUM SALTS BY SQUASH SEEDLINGS*

RODNEY H. TRUE AND R. B. HARVEY

*Bureau of Plant Industry, U. S. Department of Agriculture*

In the course of a former investigation[1] carried on with the white lupine (*Lupinus albus* L.) as a test plant, it was found that the rate of absorption of electrolytes by seedlings from solutions of the usual mineral nutrients was influenced to a great degree by the chemical character of the substances offered. In simple solutions it appeared that the usual salts of potassium were not absorbed producing rather an outgoing current of ions from the seedlings into the solutions; in magnesium solutions a small absorption took place in the more dilute solutions, while in calcium solutions absorption was much greater and took place in the most dilute solutions. It appeared from the behavior of the lupine in the solutions of calcium sulphate and calcium nitrate that in each case the quantity absorbed is limited, even though the supply may contain a large excess, and the effect of the anion appears to be subordinate to that of the Ca ion in determining the quantity absorbed.

It was found by preliminary experiments by the present authors that this condition of things does not apply to all kinds of plants. The common garden squash, sweet corn and soy bean were found to behave quite differently with respect to the anion employed with the Ca ion. In this paper the records of a series of experiments are presented showing the absorption from a series of solutions of three of the commoner inorganic salts of calcium by the seedlings of *Cucurbita Pepo* L. of the horticultural variety known as Early Prolific Marrow.

Before considering the evidence on which the conclusions here advanced are based a word concerning the method is in order. Selected seedlings obtained from seeds germinated in chopped sphagnum were grown in carefully prepared solutions contained in practically insoluble glass beakers. The concentration of ions of each solution was noted daily by taking conductivity readings by means of an accurate wheatstone bridge. The temperature throughout was

* Published by permission of the Secretary of Agriculture.

[1] True, R. H., & Bartlett, H. H. Am. Journ. Bot. 2: 278. 1915.

maintained at 18° C. by automatic control so accurate that the range of variation was seldom above four tenths of a degree Centigrade during the course of an experiment running a fortnight. The containers remained in darkness except during the short time required for the determination of the conductivity which took place in rather faint diffused light. Since it is obviously unsafe to draw conclusions from a comparison of ohms, results were always calculated to concentrations expressed as gram-normals of the salt in question dissolved in a million liters of water (grm. norm. $\times 10^{-6}$). The water was obtained by twice distilling Potomac River water from glass with electric heat in a laboratory from which gas was excluded. Each experiment was usually continued until signs of deterioration began to appear in the seedlings.

## Calcium Nitrate

Several experiments were carried out with squash seedlings in calcium nitrate solutions. Since they were in close agreement but one is presented here, that running from May first to May fifteenth, last, inclusive. The distilled water used in making up the solutions had an initial conductivity equal to that of a solution containing 11.7 grm. norm. $\times 10^{-6}$ $Ca(NO_3)_2$. Nine cultures each containing 5 seedlings and 500 cc. of solution were set up in a series ranging in concentration from 18.2 to 867.0 grm. norm. $\times 10^{-6}$. Daily observations were made until signs of exhaustion began to appear. Since in the cultures containing less than 50 grm. norm. the behavior of the seedlings varied so little in the different members of the series only a part of the record is shown here in order not to confuse the table with several nearly coinciding curves. In the curve representing the record of the culture in distilled water a dashed line is employed (Fig. 1).

It will be observed that in both distilled water and in cultures containing calcium nitrate up to a concentration of 100 grm. norm. $\times 10^{-6}$ the solutions gain in concentration for two or three days, a course which in the distilled water is followed by a very slight absorption until near the close of the experimental period. At no time, however, were the plants able to regain any considerable proportion of the electrolytes lost to the medium during the first few days.

With the dilute solutions of the salt (under 100 grm. norm.) this period of leach gradually passes over into one of active absorption as a result of which these solutions are reduced to a lower ion content than the distilled water.

As the initial salt content of the solution is increased to approximately 500 grm. norm. the slight leach seen in the weaker solutions

fails to appear, immediate though slow absorption being the rule. This intake gradually speeds up through the succeeding days, the absorption being roughly related to the original quantity of salt in the solution. This active absorption continues to the end of the experiment at which time the appearance of the seedlings and the

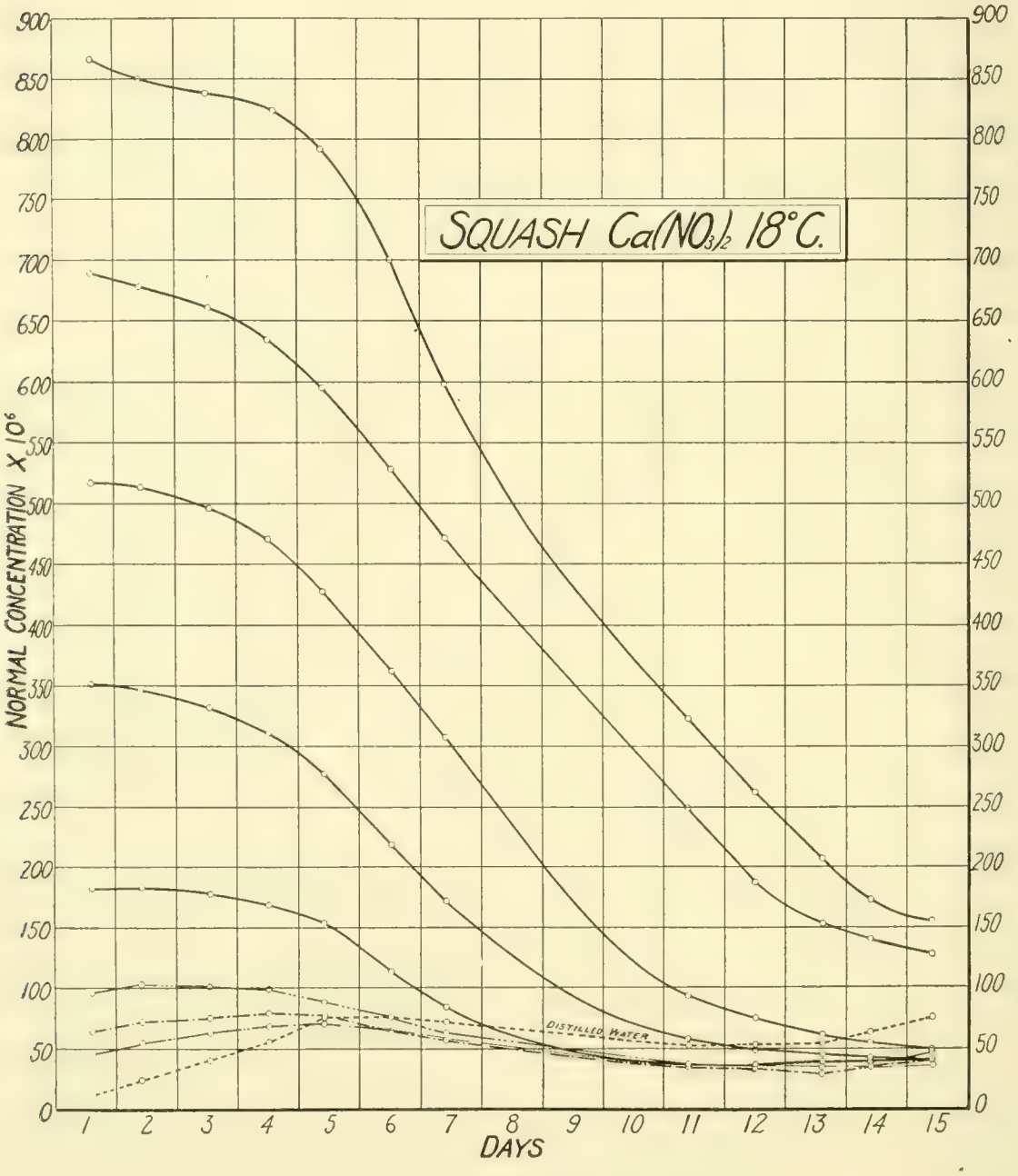



FIG. 1. For explanation see text.

diminishing absorption indicate approaching exhaustion. At this final stage of the experiment the plants have reduced the ion content of solutions of the salt to an approximately like minimum, which lies between 35 and 50 grm. norm. $\times 10^{-6}$ $Ca(NO_3)_2$. This concentration lies at about 25 grm. norm. $\times 10^{-6}$ below the concentration reached

by the distilled water, and seems to represent a fairly well-defined irreducible minimum. This point is marked by a lower ion content than the similar minimum seen in the distilled water. It seems clear that the substances giving to distilled water its conductivity are not absorbed to as dilute a minimum concentration as is calcium nitrate.

It will be noted that only in the two more concentrated members of the series are there any absorbable electrolytes remaining at the end of the experiment, and therefore only in these cultures is the total capacity of these plants to absorb this salt measured. In these cases the total absorbed salt equals 565 and 713 grm. norm. $\times 10^{-6}$ respectively.

An inspection of the graphs shows that in nearly all solutions of the salt there occurs a time at which the plants reduce the conductivity of the solution to a minimal concentration, a point that may be assumed for present purposes to represent that of maximum absorption. In some cases experiments have been closed before this point has been reached in a number of members of the series (usually the more concentrated ones), owing to the well-marked exhaustion of the plants in a number of the cultures. In such a case the absorption maximum may not have been reached, although probably in most cases it has been approached.

It is interesting to compare the original concentration of the different solutions with the corresponding concentration at the time of maximum absorption. By this means one is able to ascertain how much of the salt is absorbed or how much net loss the plants have suffered calculated at the time of greatest absorptive efficiency.

Carrying out the calculation referred to for the cultures included in this experiment the results seen in the following table (1) are obtained.

A glance shows that about 37.0 grm. norm. $Ca(NO_3)_2$ are required by five squash seedlings growing in 500 cc. of solution to enable them to protect such ions as are mobilized from their reserves against the leaching action of the distilled water. This stated in terms of the quantity of $Ca(NO_3)_2$ per plant would be about 0.00028 grm. absorbed during a period of about two weeks.

As the salt content is increased, absorption increases in approximately the same magnitude leaving an unabsorbable residue of approximately 34 grm. norm. $\times 10^{-6}$ $Ca(NO_3)_2$. This minimum is here calculated as $Ca(NO_3)_2$, but it should be clearly understood that the substances actually composing this residue may be, and probably in considerable part are, of quite other composition. Indeed, the substances indicated as $Ca(NO_3)_2$ at all stages of the experiment, especially the later ones, doubtless consist in part of other materials, largely coming by exosmosis from the interior of the test plants. The

TABLE 1

*Net Absorption by Squash Seedlings from Solutions of $Ca(NO_3)_2$*

| Original Concent. of Solution $Ca(NO_3)_2 \times 10^{-6}$ | Minimum Concent. of Solution as $Ca(NO_3)_2 \times 10^{-6}$ | Maximum Net Absorption Calc. as $Ca(NO_3)_2 \times 10^{-6}$ |
|---|---|---|
| 12.0 grm. norm. | 50.0 grm. norm. | − 38.0 grm. norm. |
| 18.2 " " | 43.0 " " | − 24.8 " " |
| 24.5 " " | 34.0 " " | − 9.5 " " |
| 36.4 " " | 32.1 " " | + 4.3 " " |
| 38.0 " " | 37.1 " " | 0.9 " " |
| 45.7 " " | 29.6 " " | 16.1 " " |
| 45.5 " " | 36.3 " " | 9.2 " " |
| 63.0 " " | 34.6 " " | 28.4 " " |
| 96.3 " " | 34.0 " " | 62.3 " " |
| 182.6 " " | 29.6 " " | 153.0 " " |
| 351.8 " " | 39.1 " " | 312.7 " " |
| 518.5 " " | 47.8 " " | 470.7 " " |
| 693.5 " " | 125.9 " " | 567.6 " " |
| 867.0 " " | 152.9 " " | 714.1 " " |

concentration indicated in any case merely states the net result of ion interchange in a given culture stated in terms of such a solution of the given salt as would have a like electrical conductivity.

As the quantity of salt is still further augmented, the unabsorbed residue increases, indicating a clear surplus of this constituent. It is interesting to note, however, that the unabsorbed residue does not increase at a rate parallel with the quantity offered; the absorption increasing also though at a lagging rate. The maximum quantity of $Ca(NO_3)_2$ absorbed by five plants out of a concentration of 867 grm. norm. $\times 10^{-6}$ is about 714.1 grm. norm. This expressed in weight of salt absorbed per seedling would be about 0.0055 grm. This may be taken to represent approximately the maximum quantity of $Ca(NO_3)_2$ absorbed by a squash seedling living in darkness in a temperature of 18° C. during the time required by the seedling to exhaust its available reserves.

## CALCIUM SULPHATE

A somewhat similar experiment was made in which calcium sulphate was used, in the hope that we might get some light on the comparative effect due to the sulphate and the nitrate anions. A series of 14 cultures was set up using squash seedlings as before covering a range of concentration between distilled water and 830 gram normals of the salt in a million liters. The experiment ran from July 12 to 23, 1916. A graphic record[2] of the course of the concentration changes in the several cultures is shown in the accompanying diagram (Fig. 2):

[2] In order not to crowd the figure only one curve representing an original $CaSO_4$ concentration less than 50 grm. norm. is given.

A glance at the curves shows that in some respects the course of absorption is markedly different from that seen in the case of $Ca(NO_3)_2$. Alike in the distilled water control and in the solutions originally containing 11.08 and 15.6 grm. norm. respectively, the solutions gain ions and not even at the time of greatest absorption are the plants able to reduce the ion concentration to that seen at the beginning of the experiment. These quantities of the salt in question are insufficient to prevent the solutions from acting practically like distilled water

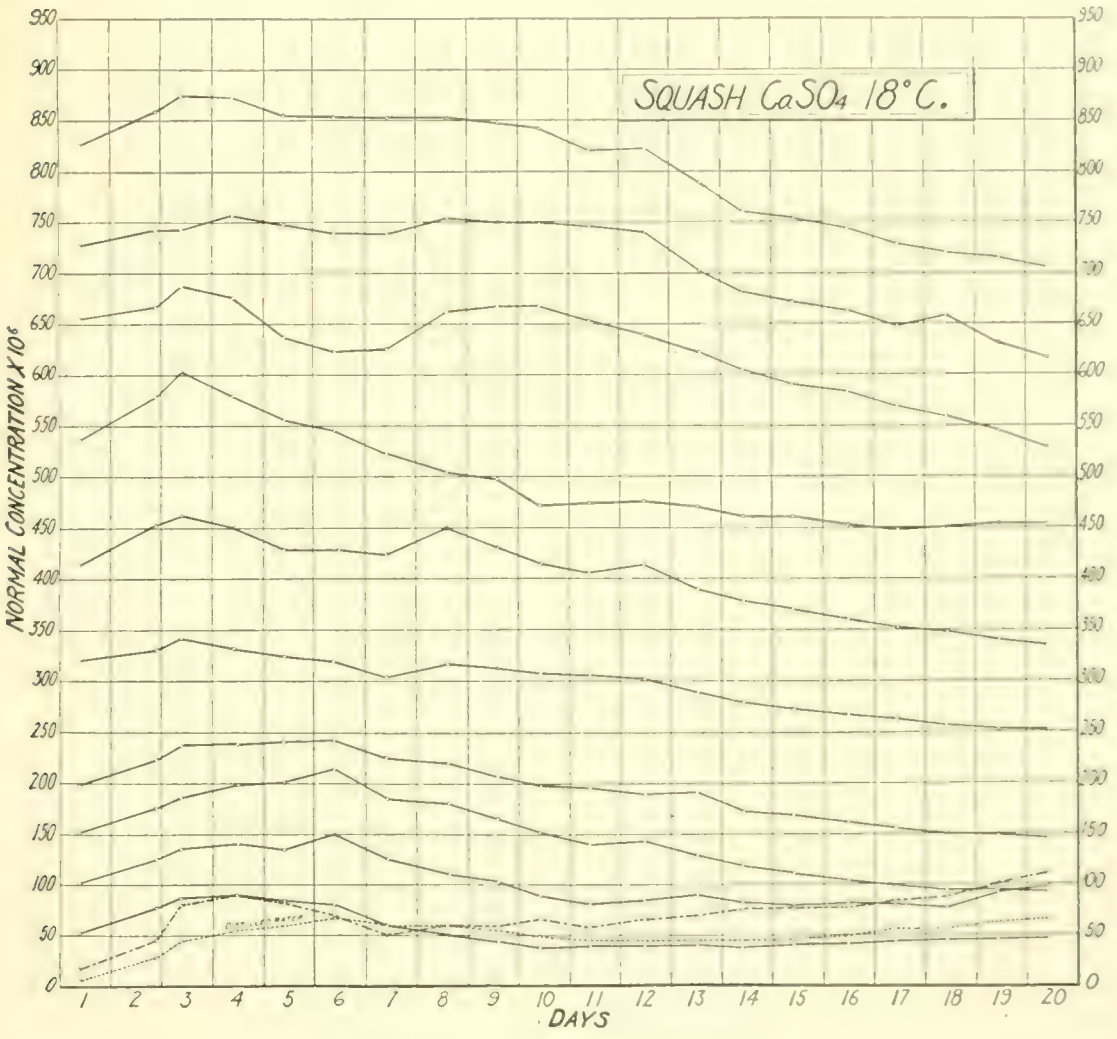



FIG. 2. For explanation see text.

by withdrawing a preponderating quantity of ions from the seedlings. When the concentration of $CaSO_4$ reaches about 30 grm. norm. in a million liters, an equilibrium of some sort seems to be established between the plant and the medium with the result that neither absorption nor leach is marked. A similar equilibrium point appears at approximately the same concentration in the case of $Ca(NO_3)_2$ solutions. It is important to note that the concentration of the calcium sulphate solutions at the time of maximum absorption in

these most dilute solutions is higher than is the case of those originally having a greater salt content, seeming to indicate that at this extreme dilution the plants are not only forced to yield ions to the solutions but are unable by reabsorbing them to reduce the concentration to a point lying much below the equivalent of 50 grm. norm. in a million liters.

As the original concentration of $CaSO_4$ is increased to 31.3 and 52.1 grm. norm. respectively absorption increases to a point showing net gains by the plants. Leaching of ions by the plants, if it takes place, is more than met here by their greater absorptive activity. This activity when greatest reduces the residual ion content markedly below that seen in the case of the originally more dilute solutions. It seems that with the addition of even slightly larger quantities of $CaSO_4$, the absorptive function becomes more active and is able more nearly to exhaust the quantity of ions offered.

As the quantity of $CaSO_4$ is increased to concentrations rising from 101.9 to 824.4 grm. norm. in a million liters the plants reduce the ion content of all solutions but absorption even at its greatest leaves a residue which increases as the quantity offered increases. Absorption, while in general increasing as the quantity of ions present increases, lags far behind the quantities offered. It thus comes about that the curve representing the residual ion content approximately parallels that representing the original ion content of the solutions.

From these data it would seem that when squash seedlings are grown in darkness at 18° C. in solutions of $CaSO_4$ alone, they are unable to absorb as many ions as they lose when the solution contains less than about 30 grm. norm. of the salt in a million liters. When the solutions contain somewhat more than this quantity of this mixture of ions the plants can reduce the more dilute members of the series to an ion content of about the concentration seen at this equilibrium point. When the supply of ions is far in excess of absolute requirements, the seedlings absorb greater quantities than in weaker solutions but the quantity of residual ions left in the solution increases in nearly the same proportion as the quantity offered.

In the following table (Table 2) are shown (1) the original concentration of each solution, indicating the quantity of ions offered in each case; (2) the concentration of each solution at the time of maximum absorption, or the residual ion content of each solution and (3) the quantity of ions absorbed from each solution at the time of maximum absorption.

TABLE 2

*Net Absorption by Squash Seedlings from Solutions of Calcium Sulphate*

| Original Concentration as Grm. Norm. $CaSO_4 \times 10^{-6}$ | Minimum Concentration as Grm. Norm. $CaSO_4 \times 10^{-6}$ | Maximum Absorption as Grm. Norm. $CaSO_4 \times 10^{-6}$ |
|---|---|---|
| 4.9 | 43.6 | − 38.7 |
| 11.08 | 61.4 | − 49.32 |
| 15.6 | 50.0 | − 34.4 |
| 31.3 | 27.9 | + 3.4 |
| 52.1 | 37.7 | 14.4 |
| 101.9 | 76.0 | 25.9 |
| 149.4 | 92.0 | 57.4 |
| 197.5 | 146.2 | 51.3 |
| 319.1 | 251.5 | 57.6 |
| 414.1 | 335.3 | 78.8 |
| 535.4 | 448.1 | 87.3 |
| 654.4 | 528.7 | 125.7 |
| 727.6 | 615.6 | 112.0 |
| 824.4 | 704.6 | 119.8 |

## CALCIUM CHLORIDE

In the foregoing experiments we have had to do with salts in which both cation and anion are required for the normal growth of higher plants, and we find squash seedlings behaving toward them in sharply contrasting ways. From solutions containing $\overset{+\,+}{Ca}$ and $\overset{-}{NO_3}$ ions root absorption is very active. When $\overset{+\,+}{Ca}$ ions are accompanied by $\overset{-\,-}{SO_4}$ ions, however, absorption is relatively small.

In view of these facts it is a matter of no small interest to test the behavior of plants in solutions in which the Ca ion is accompanied by the Cl ion.

A series of solutions was made up containing a graded series of concentrations running up to 582.4 grm. norm. in a million liters. The experiment ran from Aug. 9 to Aug. 26, 1916. A graphic record of the concentration changes observed is shown in the accompanying group of curves (Fig. 3). It is perhaps hardly necessary to do more than to point out certain of the more important features to be observed. In general a very striking similarity to the corresponding set of curves obtained from $Ca(NO_3)_2$ solutions may be noted. The solutions having an original concentration of 32.5 and less show a loss of electrolytes for the first five or six days after which time absorption begins and continues until near the end of the experiment, but in none is the loss during the early days fully regained, although in that originally containing 32.5 grm. norm. the net loss is practically negligible. At this concentration we find again evidence of a critical concentration of some sort below which the plants can not absorb and above which

they are able to do so. This required minimum quantity is probably of considerable physiological significance. At higher initial concentrations, from 53.5 to 384.0 grm. norm. loss of ions during the early days of the experiment becomes less marked as the concentration increases. Absorption usually begins more promptly and proceeds with greater speed as the quantity of ions present increases until in all cases but one the concentration of ions remaining in the solution is reduced

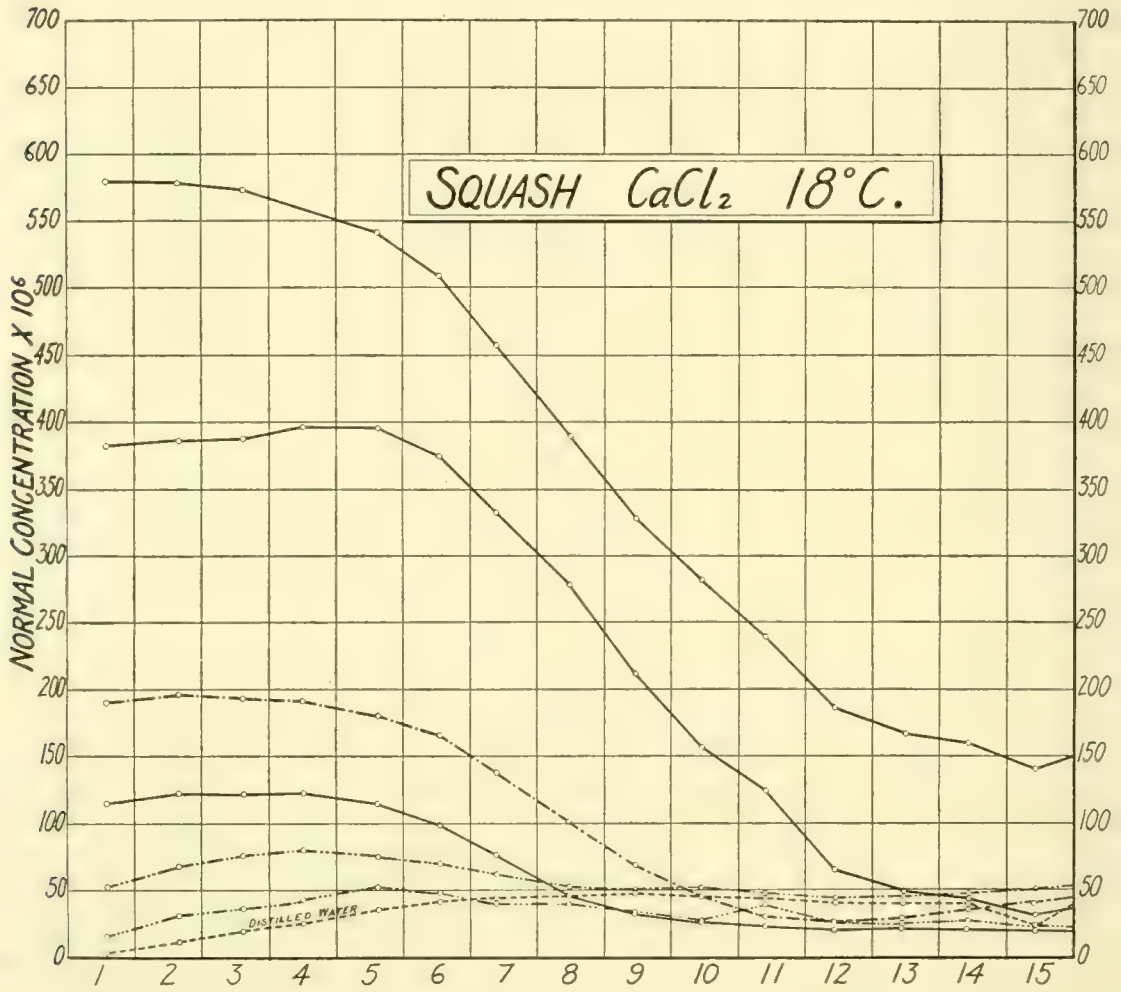



FIG. 3. For explanation see text.

to the unabsorbable minimum at an average concentration of approximately 27 grm. norm. $\times 10^{-6}$. Only when the original concentration of 582.4 grm. norm. $\times 10^{-6}$ is reached do we find the quantity of ions offered greater than can be reduced by the seedlings to the unabsorbable minimum. These relations are seen in the numerical data given in Table 3, in which the concentration relations are shown as they exist at the time of maximum absorption. Here again the similarity to the situation seen in solutions of $Ca(NO_3)_2$ is striking.

If we are justified in concluding that the depressing action of the $SO_4$ anion is responsible for the great reduction of root absorption

TABLE 3

*Net Absorption by Squash Seedlings in Solutions of Calcium Chloride*

| Original Concentration of Solution Grm. Norm. $CaCl_2 \times 10^{-6}$ | Minimum Concentration of Solution as Grm. Norm. $CaCl_2 \times 10^{-6}$ | Maximum Net Absorption as Grm. Norm. $CaCl_2 \times 10^{-6}$ |
|---|---|---|
| 4.3 grm. norm. | 38.5 grm. norm. | − 34.3 grm. norm. |
| 9.2 " " | 25.1 " " | − 15.9 " " |
| 15.7 " " | 26.5 " " | − 10.8 " " |
| 32.5 " " | 33.6 " " | − 1.1 " " |
| 53.5 " " | 42.7 " " | + 10.8 " " |
| 75.3 " " | 20.5 " " | 54.8 " " |
| 116.5 " " | 19.7 " " | 96.8 " " |
| 191.8 " " | 19.9 " " | 171.9 " " |
| 384.0 " " | 32.3 " " | 351.7 " " |
| 582.4 " " | 141.1 " " | 441.4 " " |

seen in the solutions of $CaSO_4$ when compared with that seen in solutions of $Ca(NO_3)_2$ of a similar range of concentration, we are also justified in concluding that the influence on process of absorption due to the Cl anion is as favorable as that exerted by the $NO_3$ anion.

## DISCUSSION OF RESULTS

It seems clear that for both the squash and white lupine in the seedling stage the calcium ion favors the absorption of ions. The lupine while finding this ion necessary does not absorb it in as large quantities as does the squash. The maximum requirement per culture of five seedlings of the lupine under the conditions of these experiments is not over 175 grm. norm. $\times 10^{-6}$ $Ca(NO_3)_2$ and about 125 grm. norm. $\times 10^{-6}$ $CaSO_4$.[3]

The squash on the other hand reduces an original concentration of 518 grm. norm. $Ca(NO_3)_2 \times 10^{-6}$ to 47.8 grm. norm., thus finding but a very small surplus present, and may absorb more than 700 grm. norm. when a concentration of 867 grm. norm. $\times 10^{-6}$ is offered. It is more quickly satisfied in the case of $CaSO_4$, this plant absorbing a maximum of about 120 grm. norm. only from solutions increasing in concentration up to about 825 grm. norm. $\times 10^{-6}$. It takes in therefore from an excess supply about as much $CaSO_4$ as does the lupine.

This comparison gives additional evidence of the well-known indifference of the white lupine toward calcium in several combinations.

From the evidence at hand it appears that in the presence of the Ca ion, the effect exerted by the $NO_3$ and $SO_4$ anions on absorption by the lupines is not markedly different. With the squash the anion effect comes strikingly to the front. The Ca ion accompanied by the

[3] Calculated from True, R. H., and Bartlett, H. H. Am. Journ. Bot. 2: 262 and 265. 1915.

$NO_3$ ion is from four to five times as favorable for absorption under the conditions of these experiments as the Ca ion accompanied by the $SO_4$ anion. This seems to indicate a striking and specific difference in the influence of these anions on the absorptive activities of the squash. When the Ca ion is accompanied by the Cl ion, absorption is influenced very much as in the case of Ca acting with $NO_3$ ions. The favorable effect of $NO_3$ and Cl ions is contrasted with the action of the $SO_4$ ion.

The strong influence exerted by the specific characteristics of the different species of plants is seen in the contrasting behavior of the lupine and the squash in the presence of Ca accompanied by the $NO_3$ ion.

It should be borne in mind that the probable physiological interaction of a given pair of ions is perhaps such as to make it unsafe to speak strictly of the specific action of any single ion irrespective of that of its companion ion or ions.

It is obvious from what has been here shown that any theory of cell permeability which may be framed to account for the income and outgo of the living plant with respect to electrolytes must reckon with the striking differences that exist in the behavior of plants toward even such fundamental factors as the required mineral nutrient ions.

# INHERITANCE STUDIES ON CASTOR BEANS

ORLAND E. WHITE

*Brooklyn Botanic Garden*

*Ricinus*, though a monotypic genus involving only a single widely recognized species (*R. communis*), possesses a multitudinous number of forms, which from time to time have been temporarily ranked as species. These forms breed true to many of the numerous characters which distinguish them, as shown by data obtained from growing several generations of fifty or more types in the experimental breeding plots of the Brooklyn Botanic Garden. Numerous crosses between even the most extreme types have given perfectly fertile $F_1$ and $F_2$ generation hybrids.

Hybridization studies to determine the manner of inheritance of a dozen or more of these characters have been followed through the $F_1$, $F_2$, and, in some cases, the $F_3$ generations. Several thousand plants were involved in these studies.

## Materials and Methods

Seeds of the various types were secured through Farquhar & Co. of Boston, P. Henderson & Co. of New York City, and from various botanic gardens. Many of these types are known in seedsmen's catalogues as varieties or sub-species, and these, much to my surprise (since the castor-oil plant is monoecious and wind-pollinated), bred true immediately to many of their more prominent characteristics, such as stem color, seed color and color pattern, and height. Further observations on plants of different varieties grown close together demonstrated that very little cross-fertilization took place (certainly not more than five percent), even when conditions were most favorable. This rather unexpected tendency to self-fertilization in a monoecious plant adapted apparently to wind-pollination is largely due to the slightly earlier maturity of the male flowers and to the comparative isolation of the flowers of each plant through the prevention of air currents by the large leaf surfaces. As the stigmatic surfaces of the female flowers become exposed and mature, the pollen from flowers on the same plant has already fallen or falls upon them in small clouds, thus insuring, to a large extent, self-fertilization.

Difficulty is experienced under Long Island climatic conditions in making bagged inflorescences on outdoor cultures, set a normal amount

of seed. Because of this, the $F_1$ generation plants, in some cases, were grown in isolated cultures, instead of being bagged. In this way large quantities of seed were obtained for growing $F_2$ populations. In most cases, enough seed from bagged $F_1$ plants was obtained to check up the $F_2$ results from the unbagged seed. A large number of $F_3$ families were grown from seed of unbagged $F_2$ plants. The percentage of cross-fertilization among the $F_2$ individuals appeared to be small.

## Experimental Work

### *Stem Color*

Stem color in castor beans can be roughly classified into five categories (see Plates XXIII and XXIV)—bright green, green with reddish blush on sunny side, carmine or rose red, mahogany red, and purple (dark red). The development of each type of red coloration depends, to some extent, on sunlight, particularly the red blush class. In shade, plants of this class have green stems.

These red color types are similar chemically, so far as solubility tests with their pigments are concerned, since all the red pigments are soluble in water containing a trace of chloroform, but remain insoluble in alcohol, xylol, or in pure chloroform. The red pigment is a sap color, occurring in the epidermal palisade cells in the leaf and stem (see Plate XXIII), also in parenchymatous areas of the stem, especially in the pith in some varieties. The different shades are apparently due (as observed microscopically) to different concentrations of the pigment in the cells and to a difference in the amount of pigmented cell area. From evidence thus far obtained, the writer is inclined to regard the hereditary differences between the red types as due to the presence and absence of several color dilution factors, each of which modifies the expression of a red pigment producing factor common to all, except, of course, the green-stemmed class. Still further modifications in coloration appear to be due to the presence and absence of a pattern restriction factor, in the absence of which the stems and leaves are mahogany red, or purplish red if "bloom" is present.

In crosses, red blush × other red blush varieties always gave only red blush $F_1$ and $F_2$ offspring. Red blush varieties × green-stemmed varieties and the reciprocal always gave all red blush in $F_1$ and approximately 3 red blush: 1 green in $F_2$.

| | | | |
|---|---|---|---|
| Actually obtained | 113 | red blush: | 43 green |
| Theoretically expected | 117 | " " | 39 " |

In $F_3$, seed from unbagged $F_2$ green-stemmed plants generally gave all green plants, while unguarded seed from $F_2$ red blush plants either gave all red blush or both red blush and green-stem families.

Red blush × mahogany and reciprocal gives rose or carmine-stemmed plants in $F_1$, and approximately 1 red blush: 2 rose: 1 mahogany in $F_2$, the actual figures being 47 red blush: 144 rose: 47 mahogany, theoretically expected 59.5 red blush: 119 rose: 59.5 mahogany. No $F_3$ generation of this cross has been grown, but from the above ratio the plants with rose-colored stems are expected to produce all three $F_2$ types again, while the other two types are expected to breed true.

As previously stated, there are forms with rose-colored stems that breed true. These when crossed with red blush varieties give all rose-stemmed $F_1$ plants, indistinguishable from their rose-stemmed parent. In $F_2$, these produced 429 rose: 145 red blush, the theoretically expected proportions being 430.5 rose: 143.5 red blush.

Associated with the types of stem coloring are pigmented areas in other parts of the plant. The mahogany-red-stemmed plants have mahogany-red leaves and fruits. The rose- and red-blush-stemmed types have green leaves with red or reddish-green midribs. The dark purplish-red- (mahogany bloom) stemmed plants have dark purplish-red leaves and fruits. Plate XXIII is a much enlarged micro-photograph in natural colors showing the pattern and distribution of the pigmented areas in the leaf of the mahogany type. The pattern resembles one of the mottling patterns in castor-bean seed coats, and possibly may be due to the same cause. It occurs only in the forms with dark red or purplish-red leaves and stems, and may be regarded as resulting from the absence of the pattern restriction factor previously mentioned.

### *Bloom*

Bloom, similar in appearance to that on grapes, in castor beans consists of a scale-like waxy substance, which, under the microscope, resembles a piece of cracked frozen ground. It is easily rubbed off. This covers the whole plant and is especially noticeable on the stems and fruit capsules. In some varieties, it is produced more freely than in others. Many forms are known which breed true to its absence. When it occurs on plants with mahogany stems, a dark purple or purplish-black effect is produced (see Fig. *D*, Plate XXIV).

Crosses of bloom × no-bloom give either complete or partial dominance of bloom in $F_1$. In $F_2$, approximately 3 with bloom: 1 no-bloom were obtained (actual numbers being 1,108 bloom: 377 no-bloom, the theoretically expected being 1,113 bloom: 371 no-bloom). In $F_3$, seeds from unguarded $F_2$ plants without bloom produced only plants without bloom. Seeds from unguarded $F_2$ plants with bloom either bred true in $F_3$ or gave 3 bloom: 1 no-bloom families. In one

cross of bloom × no-bloom, the $F_1$ plants had bloom, but were only lightly covered as compared with their "bloom" parent. In $F_2$, the plants approximated a ratio of 3 bloom: 1 no-bloom as usual, though many of those with bloom were lightly covered as in $F_1$.

*Dehiscent and Indehiscent Seed Pods*

The seed pods or seed capsules of *Ricinus*, in most varieties, are dehiscent, the seeds being thrown out of the mature ripe capsule with great force. These are known as "poppers" in regions where the plant is cultivated commercially. A few varieties have indehiscent capsules, the seed being retained within the pod for several months. This characteristic considerably reduces the cost of harvesting the beans, as only two or three collections a season are necessary, whereas "popper" varieties must be harvested twice a week or more, to prevent loss. The castor-bean plant matures its seed over a very long season. The "non-popping" variety with which the writer experimented has thin-walled, comparatively brittle capsules, while all the popping varieties have capsules with thick, leathery walls. The dehiscent characteristic is probably due to cells similar to those found in the fern sporangium, which rapidly lose their moisture content when the capsule matures and contract, thus breaking apart the capsule and expelling the seed.

Crosses of "popper" with the "non-popper" variety gave all "poppers" in $F_1$ and approximately 9 "popper": 7 "non-popper" in $F_2$ (the actual figures being 343 pop.: 259 n.-pop., the theoretically expected being 338.4 pop.: 263 n.-pop.).

In $F_3$, seed from unguarded $F_2$ "popper" segregates gave either all "poppers," or "poppers" and "non-poppers."

Seed from unbagged "non-popper" $F_2$ segregates produced in most cases only "non-poppers." The "popper" and "non-popper" varieties involved in the crosses were *very* distinct, but the $F_2$ populations were somewhat difficult to classify, as many of the "non-poppers" would, under very favorable conditions, slightly pop. These were usually thin-walled, brittle capsules, showing, perhaps, that the nature of the capsular tissue (thick, leathery or thin and brittle) modified the "popping" or "non-popping" characteristics. On the assumption that two pairs of characters are concerned in this cross, each of which is primarily determined by the presence and absence of a single factor, the results may be interpreted by regarding the "popper" character as due to the presence of both the factor for popping (A), and the factor for thick, leathery capsules (B). In the presence of A and the absence of B, the capsules would have thin, brittle tissues, but pop slightly, although not sufficiently to class them as "poppers." In the

presence of B and absence of A, the capsules would be thick and leathery, but non-popping. When both A and B are absent, the capsules would be thin, brittle, and non-popping. On this provisional hypothesis, "non-poppers" of the aB class crossed with those of the Ab class would give all AB or "poppers" in $F_1$ and a 9 : 7 ratio in $F_2$. The two types used in the above-recorded crosses would be represented by the formulae

AABB = "poppers,"
aabb = "non-poppers."

Crosses of these would give a 9 : 7 $F_2$ ratio, such as that actually obtained.

*Seed-coat Colors*

Seed-coat colors in castor beans are white, brownish yellow, various shades of red, gray, brown, and black. With one exception, all forms, so far as the writer knows, have seed coats in which the ground color is modified by one of several mottling patterns, although the mottling patterns are inherited, as in garden beans, independently of the ground color. The nearest approach to a self color in the writer's collection is a black-seeded variety having in some cases very few mottling marks and in others none at all. Efforts have been made to discover a self-colored white-seeded variety, but so far with no success.

In crosses, chocolate brown is dominant over black, red, white and gray. No $F_2$ data are available from any crosses excepting those of red × brownish gray and its reciprocal. The $F_1$ is brown on a gray background. In $F_2$, segregates of various degrees of redness appear as a minority. By counting all those $F_2$ segregates with a red cast, an approximation to a ratio of 3 brownish gray : 1 reddish gray is obtained. The actual results are 172 non-red : 40 reddish gray or red, the theoretically expected results being 159 non-reds : 53 red gray. No reds as brilliant as the grand parental type appeared, showing that more than a single pair of factors is involved.

In $F_3$, seed from unbagged $F_2$ light red segregates gave all light reds in the majority of cases. Seed of the same kind from medium red $F_2$ segregates also bred true. Seed from unbagged brown $F_2$ segregates gave browns of various shades in some cases in $F_3$, while in others, browns, reds, and brown grays were produced. Reds as brilliant as the red ancestor were secured from red $F_2$ segregates.

At least three types of seed-coat color mottling can be distinguished definitely in castor-bean seeds. One is coarse-veined, one is fine-veined, dotted and splotched, while the third is characterized by a very few large splotches. When the seed-coat is black, the mottling

is obscured. As in the case of the stem colors, the different types of mottling appear to involve the presence and absence of several pairs of restriction factors. Only two of these patterns have been studied in detail. These are the coarse- and fine-veined types. Crosses between coarse and fine always give in $F_1$ all fine, indistinguishable from the "fine" pattern parent. In $F_2$, approximately 3 fines : 1 coarse are obtained, the actual figures being 163 fine : 49 coarse (theoretical expectation 159 fine : 53 coarse). Unbagged $F_2$ segregates having coarse mottled seed generally breed true in $F_3$, the few cases where plants with fine mottled seeds have appeared being undoubtedly due to foreign pollen contamination. Unbagged $F_2$ segregates with fine mottled seeds either bred true in $F_3$ or gave both fine and coarse-mottled progeny. Coarse-mottled $\times$ the large splotched type gives a dominance of the former in $F_1$. No $F_2$ progeny have been grown.

### Interpretation

The inheritance of five of the sets of characters described in preceding pages—green and red blush stems, red blush and mahogany stems, red blush and rose red stems, bloom and no-bloom, fine and coarse seed pattern—so far as the $F_1$ and $F_2$ data are concerned, are most simply interpreted as due to the presence and absence of a single genetic factor in each case, making in all five genetic factors. The inheritance of dehiscent and indehiscent capsules is assumed to involve primarily two pairs of factors. No evidence of *close* linkage was found between any of these seven pairs of factors, although the data were taken with this end in view.

### Seed Shape and Dimension

Castor-bean seeds differ as to shape in being oval or orbicular (about as long as broad). In crosses between varieties breeding true to the two types, the $F_1$ plants are all oval seed, while in $F_2$, orbicular seeds are present in considerably over one fourth of the progeny suggesting a 9 : 7 ratio.

Varieties of *Ricinus* vary remarkably in their seed dimensions and weight. Some of the commercial varieties have seeds less than a centimeter long, which run about 4,550 to a pound of 450 gm., while the seeds of some of the large Zanzibar ornamental types are over 2.5 cm. long and run only 450 to a pound. Between these are numerous forms breeding true to almost every gradation in size and weight.

A large number of crosses between these types have been made, the $F_1$ plants showing various degrees of intermediacy. All the

different $F_1$ plants of each were practically uniform as to seed size (see Plates XXV, XXVI, and XXVII).

Most of the large-seeded forms and some of the very small-seeded forms (with indeterminate growth period) require a long season to produce mature seeds, so that even when $F_2$ populations were started in the greenhouse in pots several months before planting out, only about two thirds of the segregates matured seed. One year, attempts to overcome this difficulty by growing the plants in 10 cm. pots for a year were unsuccessful. The difference in seed maturity between the outdoor and these pot-grown plants was very slight. Because of these difficulties, several of the $F_2$ populations shown in Plate XXVII represent only part of the segregates—the small- and intermediate-seeded classes. In $F_2$ populations from small $\times$ large seed or the reciprocal, small-seeded types similar to the small-seeded grandparent and even smaller were obtained in every case, while in some of the crosses involving nearly complete $F_2$ populations (Plates XXV, XXVI), the large-seeded type was also obtained. In all crosses, as expected from studies of size characters in maize, poultry, and other plants and animals, numerous intermediates were present, so that a complete $F_2$ population represented a gradating series ranging from those similar to or smaller than the small-seeded parent to those similar to the parent with large seeds.

Seeds from unbagged $F_2$ small-seeded and large-seeded segregates have given similar $F_3$ progeny, showing the extremes to breed true. Various $F_2$ intermediates have also bred true in $F_3$, while other intermediates have given the whole $F_2$ series again. Still others have shown very much less variation.

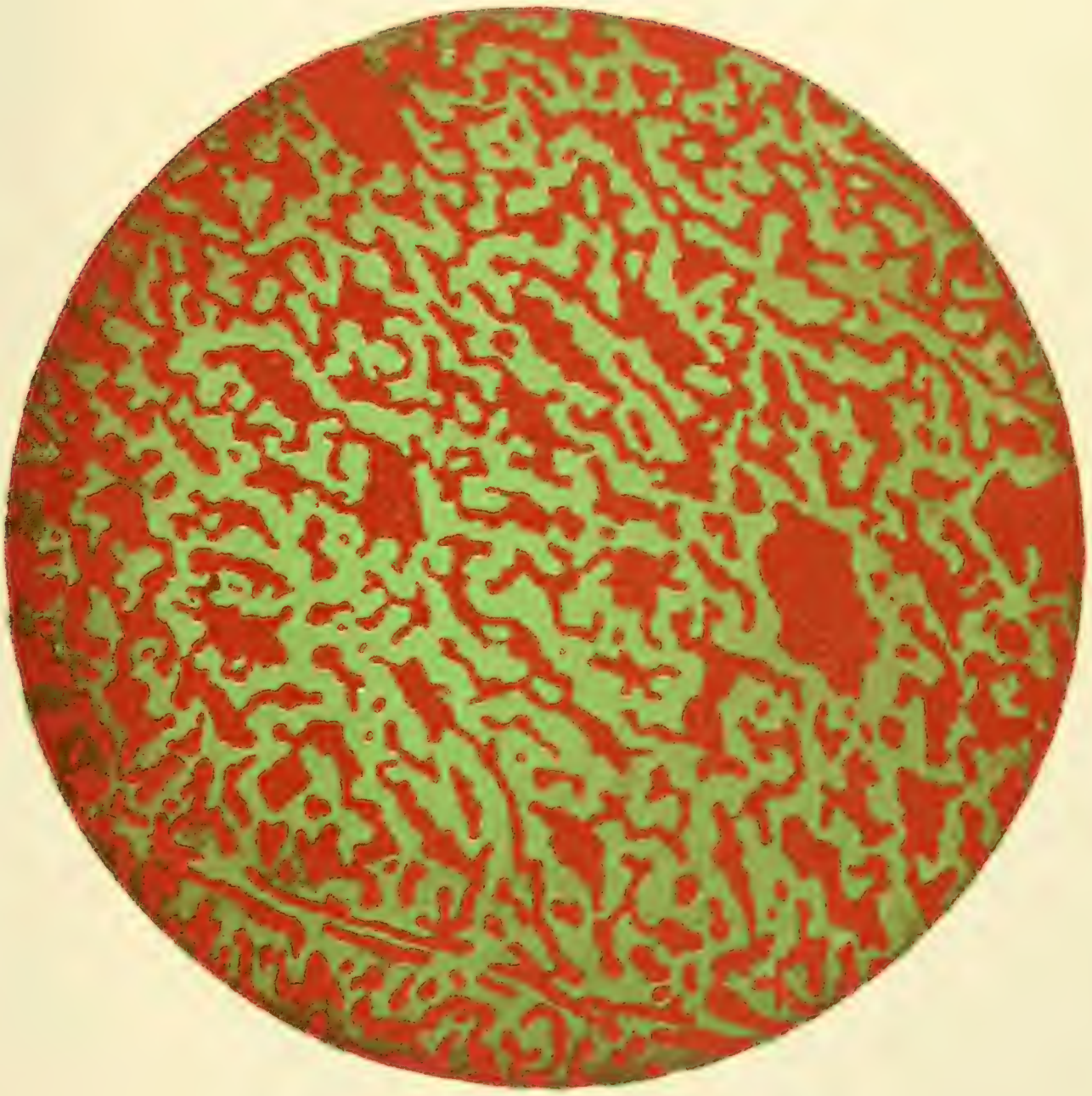
## Other Characters

Numerous characters, other than those described in preceding pages, have been studied from the standpoint of heredity, but not in sufficient detail, to admit of interpretation. Crosses between low-growing (dwarfs), early seed-maturing types with determinate growth, and tall, late-maturing types with indeterminate growth gave intermediates in $F_1$, which in $F_2$ gave all three types, though accurate classification so far has been impracticable. Crinkled, much notched leaved types crossed with ordinary leaved types gave either dominance of the ordinary type or intermediates in $F_1$. Some types have a loose, few-seeded fruiting spike, while others have a dense compact spike with a larger number of pods. Crosses between them give either intermediates or dominance of the loose spike. In $F_2$, both types reappear, together with many intermediates.

## Heterozygosis

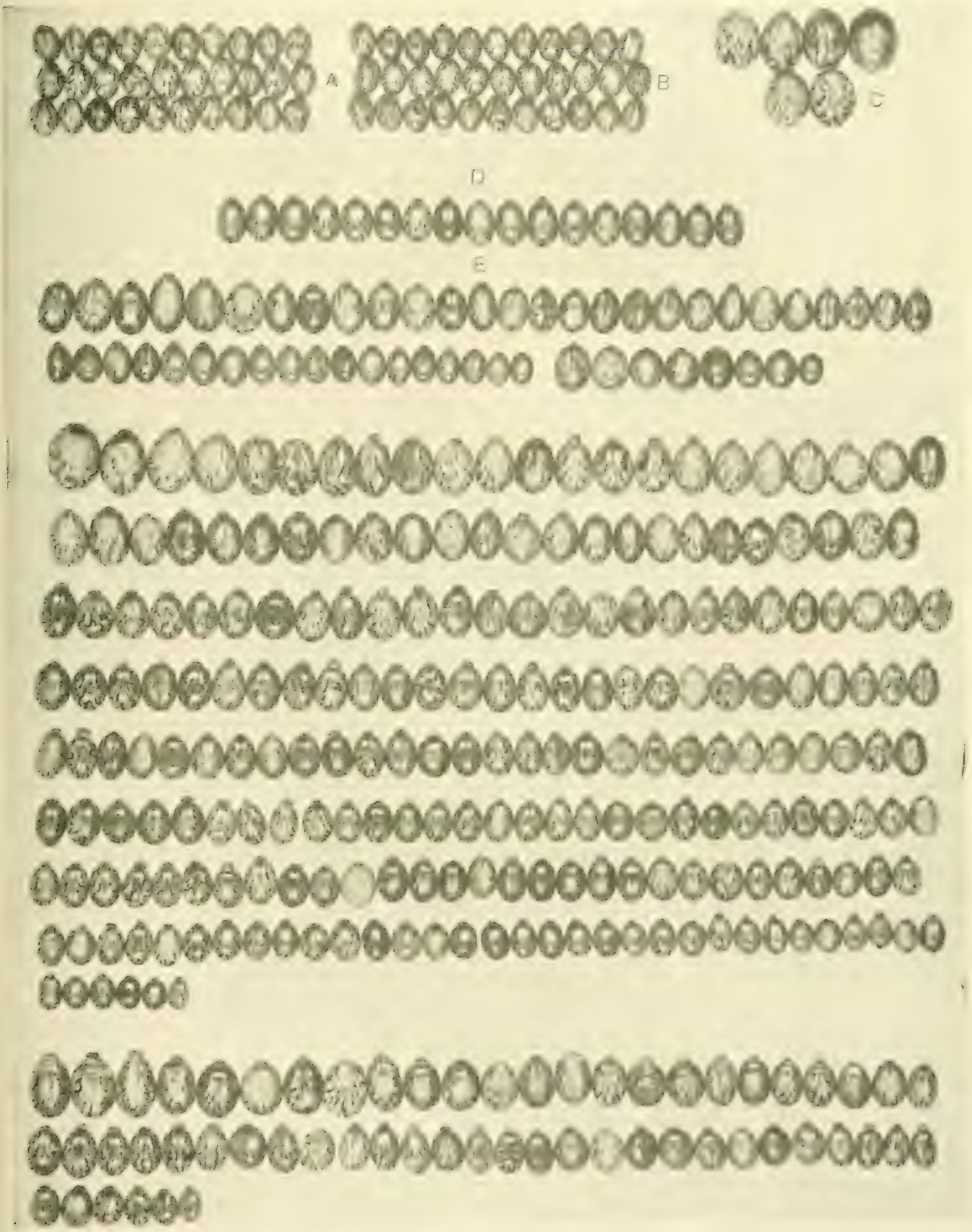
$F_1$ hybrids between several of the forms produced, as in many maize crosses, a much larger amount of seed than either parent, the environment being practically the same for all. $F_1$ hybrids between still other forms, however, failed to show this increased productivity. This is also true of maize $F_1$ hybrids.

This increased productiveness in $F_1$ should be, as in the case of maize and tomatoes, of great commercial value, since crossing castor-bean varieties, where no particularly accurate results are desirable, is very simple and could be done rapidly. Plants of the two types to be crossed could be grown separately and one lot used entirely as a pollenizer. A large quantity of pollen from the same spike matures at the same time. Hence, these spikes could be cut off when nearly mature and laid on paper sheets till the pollen was shed—a matter of a day or two. The pollen could then be collected in a powder gun or similar device and shot over the newly matured pistils each morning. The male flowers on the plants used as seed-bearers, for the most part, can be easily rubbed off without injuring the flower spike. The amount of selfed seed by this method would be very small, most of the mature seed being crossed. As ordinarily planted commercially, one bushel of beans running 1,500 beans to the pound will plant anywhere from 6 to 40 acres, depending on the distance apart and the number of beans planted per hill (1–3 beans). Some of the commercial varieties run as high as 3,000 beans or more per pound. Castor beans produce from 10 to 40 bushels per acre, depending on the variety, soil, climate and length of frostless season. With these facts in view, it seems unnecessary to urge the commercial importance of using $F_1$ generation hybrid seed produced by the method mentioned above. Experiments to determine which varieties crossed together would give the greatest yields in a given locality should be made in regions where the beans are grown commercially, since, as previously stated, there is great variation in varieties as regards this characteristic. This characteristic of increased productivity in $F_1$ progeny of certain varieties, combined with such characters as "non-popping" and high oil content, should help toward putting castor-bean growing on a better commercial basis in this country. No experiments regarding increasing the oil content through "selection," so far as the writer knows, have been made. Varieties with seed yielding 30 to 45 percent oil are said to be already common commercially. Experiments with, and chemical analysis of the innumerable varieties would possibly give us strains with a much larger oil content.

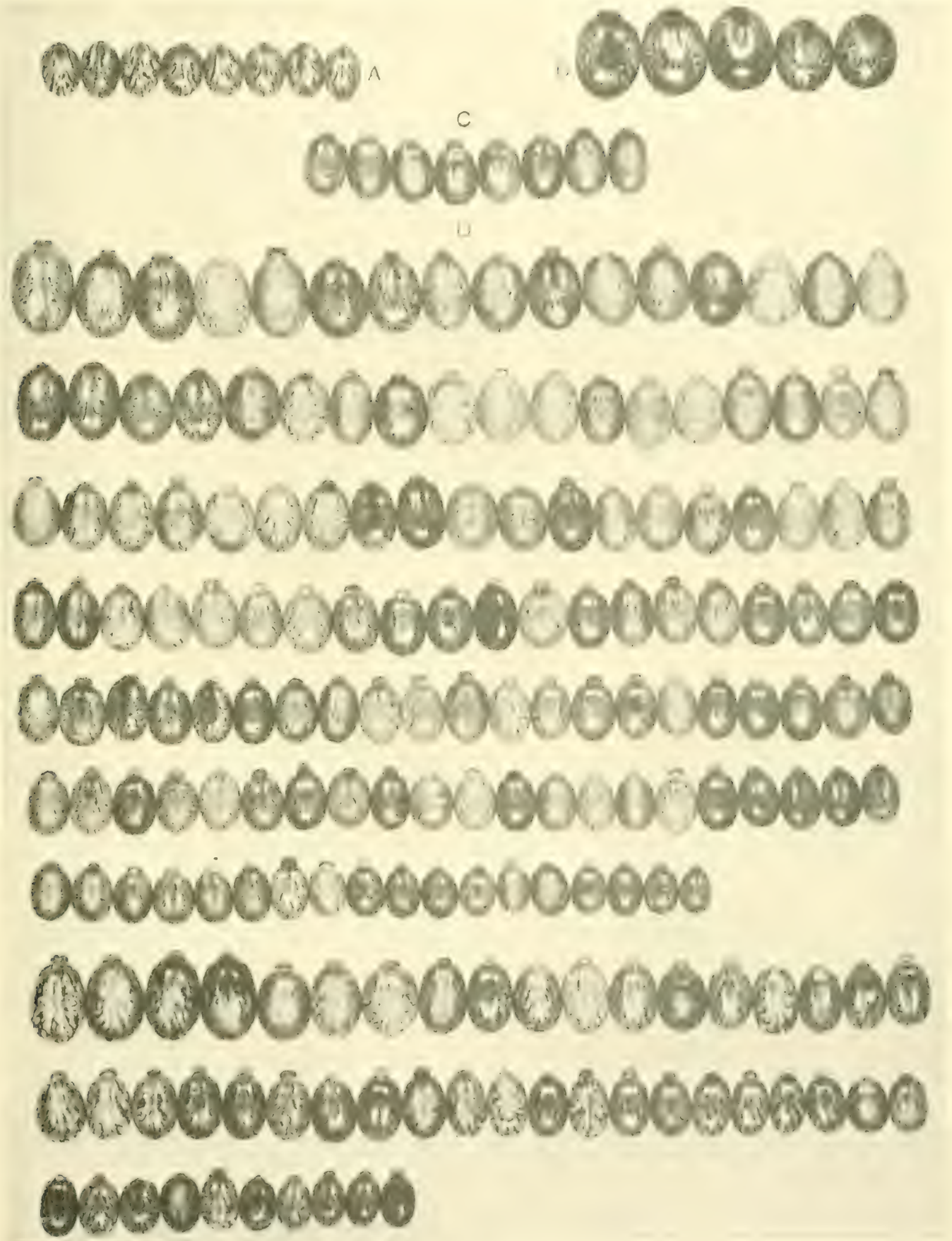


White: Inheritance

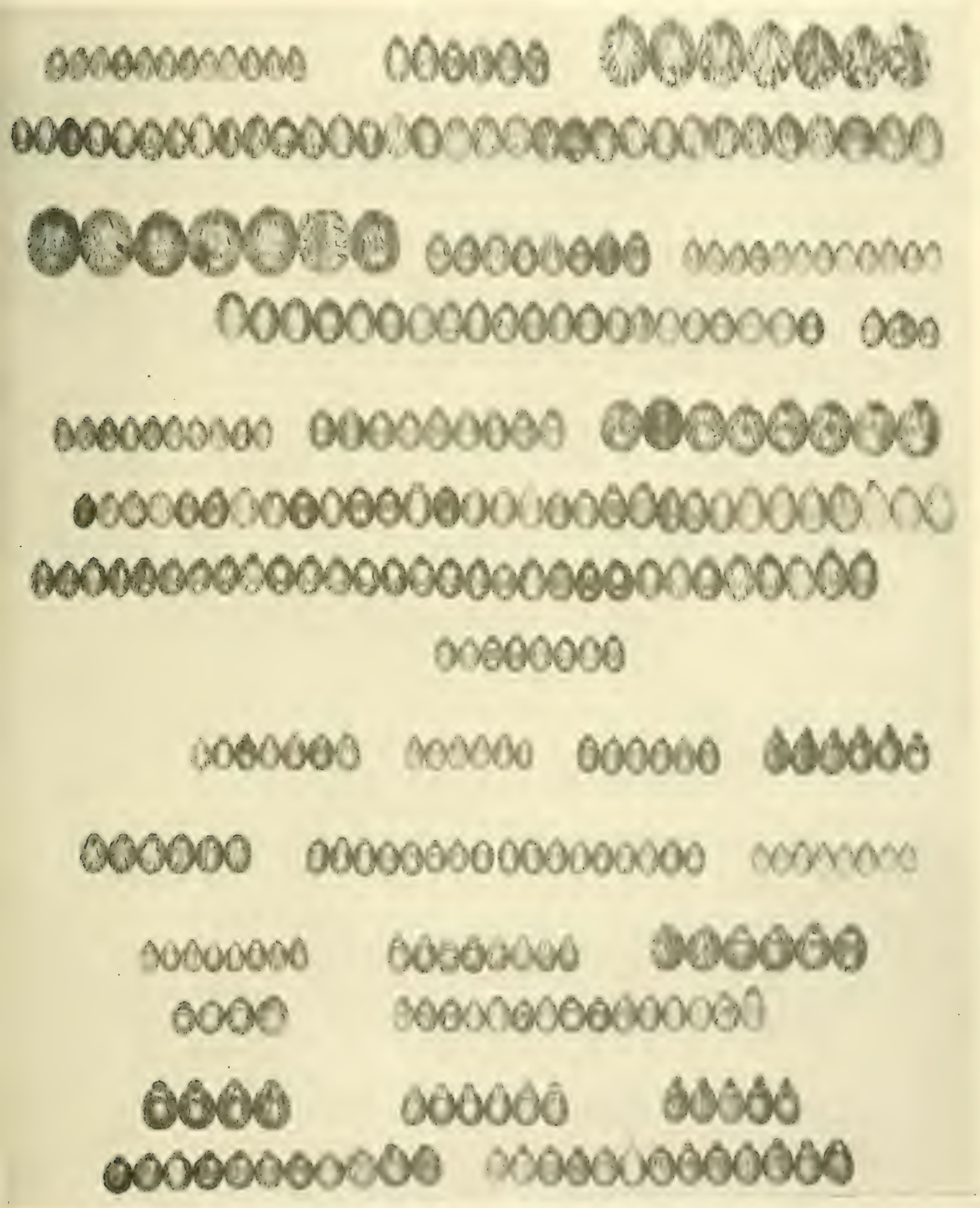
WHITE: INHERITANCE STUDIES ON CASTOR BEANS




WHITE: INHERITANCE STUDIES ON CASTOR BEANS




WHITE: INHERITANCE STUDIES ON CASTOR BEANS



White: Inheritance Studies on Castor Beans

WHITE: INHERITANCE STUDIES ON CASTOR BEANS

## EXPLANATION OF PLATES XXIII–XXVIII

PLATE XXIII is a microphotograph of a highly magnified portion of leaf epidermis of the mahogany type showing the red pigment pattern.

PLATE XXIV illustrates the various stem colors. Fig. *A* is red blush and green bloom; Fig. *B* is green; Fig. *C* is red blush and green without bloom; Fig. *D* is mahogany red or dark red-purple with bloom; Fig. *E* is mahogany or dark red without bloom; Fig. *F* is rose or carmine red.

PLATE XXV illustrates inheritance of seed dimension. *A*. The ovule or maternal parent is represented by 30 seeds, each seed representing a random selected sample from a single plant, showing the degree of variation in seed dimension within the variety. *B*. 30 seeds selected at random from a single plant of the maternal parent variety, showing the degree of variation in seed dimension on the same plant. *C*. 6 seeds representing 6 plants of the paternal parent. *D*. $F_1$ progeny. Each $F_1$ seed is a random selected sample from a single plant, illustrating the uniformity in seed dimension of the $F_1$ progeny. *E*. Three $F_2$ families are shown, each separated by a white line. Each $F_2$ segregate represented by a single random selected seed.

PLATE XXVI illustrates inheritance of seed dimension and coarse and fine pattern. *A*. Maternal parent. *B*. Seed similar to paternal parent in size, seed coat pattern and in seed shape. *C*. $F_1$ progeny. Note the uniform appearance both as to size and pattern in the $F_1$ progeny. *D*. $F_2$ progeny. Only one $F_2$ family is represented. The coarse and fine pattern segregates are arranged in a separate series.

PLATE XXVII. A series of crosses illustrating inheritance of seed dimension, pattern and seed shape. The different crosses are separated by a white line. Each seed was selected at random and represents a single plant. Only part of the $F_2$ progeny of these families are shown, as the large-seeded segregates did not mature. In all these crosses excepting cross no. 4 (from the top), the maternal parent is placed on the left, the paternal on the right, and the $F_1$ generation between them in one row, while the row or rows below represent the $F_2$ progeny. In cross no. 4, the group of 7 beans on the left is all that matured of an $F_2$ progeny, the $F_2$ parent and two grandparents of which are in the same row and arranged as mentioned above, the ovule parent on the left, etc. In some of the $F_2$ populations, attempts to classify the beans as to shape have been made.

PLATE XXVIII. *A*. Two leaf types. Varieties with the crinkled, notched type being much more ornamental than the other. *B*. Loose and compact forms of fruiting spikes. The compact form associated with certain other characteristics in a variety means greater productiveness.

New York Botanical Garden Library
3 5185 00289 4499